EARLY UPPER CAMBRIAN (MARJUMAN) LINGULIFORMEAN BRACHIOPODS FROM THE DEADWOOD FORMATION

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By

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Abstract

The Deadwood Formation is an Upper Cambrian to Lower Ordovician succession of sandstones, shales, siltstones and limestones that blanketed central western North America during the initial Phanerozoic transgression. This transgression led to a broad, shallow epeiric sea which onlapped the Transcontinental Arch to the east and was protected on its western—seaward—side by a system of carbonate platforms now exposed in the Rocky Mountains. The Deadwood Formation is mostly a subsurface unit, but several exposures exist in the northern Great Plains due to uplift by Eocene igneous intrusions. Linguliformean brachiopods were recovered from two areas: the Black Hills of South Dakota, and two subsurface cores from Alberta and Saskatchewan.

Forty-five species of linguliformean brachiopods assigned to twenty-eight genera were recovered from these localities and described. Giving provisional names, one new family, Holmerellidae, one new subfamily, Neotretinae, five new genera, *Amplitreta, Dianabella*, *Ganotoglossa*, *Holmerellus*, and *Vangaporosa,* are erected and seventeen new species are described: *Amplitreta cyclopis, Amplitreta elongata,* aff. *Anabolatreta tora, Canthylotreta parislata, Curticia pustulosa, Dianabella artemesia, Ganotoglossa leptotropis, Holmerellus convexus, Holmerellus, acuminatus, Holmerellus limbatus, Kotylotreta nupera, Linnarssonella tubicula, Opisthotreta nuda, Rhondellina albertensis, Tropidoglossa costata, Quadrisonia? sigmoidea,* and *Vangaporosa dakotaensis*. The family Holmerellidae is distinguished by pitted larval shells and smooth postlarval shells, a feature that is unique in the Linguloidea. The composition of the new subfamily Neotretinae recognizes the evolutionary relationship of the genera *Neotreta* and

Rhondellina, which are more closely related to each other than to any other acrotretid genera.

Based on a comparison of the brachiopod assemblages with similar faunas from Australia and elsewhere in Laurentia, the sections studied are determined to be late Marjuman (early Late Cambrian) to early Sunwaptan (middle Late Cambrian) in age. The subsurface faunas provide the first biostratigraphic dates for any part of the Deadwood Formation in Canada. Faunas from South Dakota come from strata near the base of the formation and below the first trilobite occurrences, this giving a more refined age for the transgression in South Dakota.

A faunal connection between Australia, Kazakhstan and Laurentia appears to have existed, based on the large number of taxa shared between these cratons, and a map of hypothetical large-scale circulation patterns in the Late Cambrian is proposed. It aims to account for the distribution of planktonic brachiopod larvae by adapting patterns of equatorial symmetry in gyre cells to presumed continental positions at that time.

A large number of shells with perforations assumed to have been caused by predators were recovered from two localities in South Dakota, and represent the first evidence of predation of fossil lingulids. Two types of perforations were identified: round holes with sharp, non-beveled edges, and irregularly shaped holes with chipped edges. The former hole type is attributed to either steady pressure applied over time (e.g. boring) or to a swift, piercing percussive strike. The latter hole type is attributed to a smashing percussive strike with a blunt appendage. Based on criteria established by the proposed attack-mode models, various hypothetical animals are discussed as potential linguliformean predators. While the evidence for these predators is circumstantial, it

indicates a more complex benthic paleoecology that had hitherto been envisaged for the Upper Cambrian.

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Part D: Early Late Cambrian linguliformean brachiopods from the Deadwood Formation of South Dakota

Introduction

One of the first people to study brachiopods in North America was James Hall, of the United States Geological Survey, who produced a prodigious body of work between 1843 and 1894, first on the fossils of the eastern U.S., and then the western territories, as the U.S.G.S. began to explore the frontier. Hall's reports described many genera and species of inarticulated, organo-phosphatic shelled brachiopods, now known as the Linguliformea, and laid the groundwork for their further study in the late nineteenth century by C.D. Walcott, C. Schuchert, G.F. Matthew, and F.B. Meek, among others. Walcott, in particular, made an unparalleled contribution to the study of inarticulates, culminating with the publication of his exhaustively researched two-volume monograph, Cambrian Brachiopoda (Walcott, 1912), which has remained a valuable reference to this day.

Hall's Canadian counterpart, Elkanah Billings, of the Geological Survey of Canada, also produced an impressive palaeontological contribution, documenting the fossils of Canada between 1857 and 1874. Though he did extensive research on the Brachiopoda, Billings' work never initiated a tradition of research of the inarticulates, as Hall's did in the U.S. As a result, with the exception of some work done on Canadian brachiopods by Walcott, linguliformean faunas in Canada remain largely unknown, and what little had been done is now out of date.

There was a lull in the study of inarticulate brachiopods in North America until the 1940's, when Charles Bell, North America's first dedicated inarticulate specialist, applied a technique of etching limestone in acetic acid to recover the phosphatic shells

from the insoluble residue (Bell, 1948). This allowed a detailed examination of the morphological structures of valve interiors, which proved to be critical, as the exteriors of linguliformean shells tend to be very conservative and difficult to differentiate. Because many of the linguliformeans, particularly the acrotretids, are micromorphic it is impossible to prepare them manually by "crack-out" from limestones, to which they are largely restricted. Furthermore, because of their small size, acrotretids are extremely difficult to detect in hand samples of rocks, and their presence can usually only be detected by chemical preparation. Thus, study of the Linguliformea was previously limited to the larger lingulids, which are often prominent on the bedding surfaces of clastic rocks.

Bell's acid etching technique sparked renewed interest in the study of inarticulates, and many subsequent papers describing linguliformean faunas were written in the following decade by C. Lochman, A.R. Palmer, and G.A. Cooper. Cooper's contribution to brachiopod palaeontology was particularly impressive, and in his two-volume monograph, Chazyan and Related Brachiopods (Cooper, 1956), the single greatest contribution to the field since Walcott's Cambrian Brachiopoda, he described and named most of the species and genera of Ordovician linguliformeans known in North America today.

Up to this point, most of the palaeontologists studying Cambrian linguliformeans, aside from Bell, were trilobite specialists who described some of the brachiopod fossils they found alongside their trilobites. Thus, the research done on the inarticulates was almost exclusively taxonomic, with little discussion of their palaeoecology. This remained the case until the 1960's when A.J. Rowell succeeded Bell as North America's

premier linguliformean specialist. In addition to describing new faunas, and establishing many new taxa of inarticulate brachiopods, Rowell also concerned himself with their evolution, habitat diversity, and biogeography. Rowell is now retired, and despite his extensive research and publication, linguliformean faunas in many regions of the United States have yet to be described.

Study of fossil linguliformeans in Europe began in the early to mid-nineteenth century with the works of J. Barrande, C.E. von Eichwald, C.H. Pander, E. de Verneuil, and S.S. Kutorga, to name just a few, though the earliest study of the living genus *Lingula* was written in the late eighteenth century (Bruguière, 1797), and the living brachiopod, *Lingula anatina*, was described shortly thereafter (de Lamarck, 1801). The groundbreaking work of these and other prominent early palaeontologists led to a small, but on-going tradition of linguliformean research in Europe that never occurred to a similar degree in North America or elsewhere. Though there was a lull in the early twentieth century, by the middle of the century there was a renewed surge of research by O. Kuhn, K. Sdzuy, A. Williams, and V. I. Gorjansky. These palaeontologists trained a new generation of specialists who have spawned a current renaissance in linguliformean research.

Current Research

There is, at present, a small number of palaeontologists specializing in the Linguliformea, whose research is focused mainly in central and eastern Europe. M.G. Bassett, G. Biernat, L.E. Holmer, S. Koneva, M. Mergl, L.E. Popov, and G.T. Ushatinskaya have made significant progress in documenting the faunas of Russia,

Kazakhstan, Poland, Estonia, and Scandinavia. Holmer and Popov, in particular, have made fundamental contributions to Cambrian and Ordovician biostratigraphy, using linguliformean fossils. Sir Alwyn Williams remained active long after retiring, and continued to expand the understanding of brachiopod shell microstructure until his death in 2004.

With the recent increase in linguliformean research, much progress is being made in understanding the evolution of the group, and has resulted in the reorganization of the phylum Brachiopoda into four subphyla, one of which incorporates the former phylum Phoronida (Williams et al., 1996; Williams et al., 2000). Likewise, the Linguliformea are becoming widely recognized as having important potential as biostratigraphic and biogeographic indicators in Cambrian and Ordovician strata. Present knowledge of linguliformean palaeobiogeography and palaeoecology is limited due to lack of available data, particularly in North America, a situation that is unlikely to be remedied soon, as there are currently no other specialists working in North America, and linguliformean fossil faunas are, as yet, undescribed from most of the continent.

This thesis describes the linguliformean fauna from the Deadwood Formation in the Williston Basin region of Laurentia. In addition to a taxonomic description of the fauna, it also provides new information on predation of brachiopods during the Late Cambrian and discusses the palaeobiogeographical relationships between the Deadwood fauna and those previously described from Kazakhstan and Australia. The main body of the thesis (chapters two to four) consists of manuscripts prepared for publication. Chapter two: PREDATION OF LATE CAMBRIAN LINGULIFOREAN BRACHIOPODS FROM THE DEADWOOD FORMATION OF SOUTH DAKOTA, is

to be submitted to Lethaia. Chapter three: MIDDLE TO UPPER CAMBRIAN LINGULIFORMEAN BRACHIOPODS FROM THE DEADWOOD FORMATION OF SUBSURFACE ALBERTA AND SASKATCHEWAN, CANADA, was published in Journal of Paleontology vol. 77 no. 2, March, 2003. Chapter four: EARLY LATE CAMBRIAN LINGULIFORMEAN BRACHIOPODS FROM THE DEADWOOD FORMATION OF SOUTH DAKOTA is to be submitted to NRC Press monograph series.

Chapter two discusses the predation of linguliformeans based on one hundred and forty shells perforated by two types of holes. The different types of perforation implies that different predators using different types of attacks were preying upon linguliformeans. An attack-mode model is proposed to simulate the various attacks that could produce the described perforations, and various predators that might have been capable of making such attacks are suggested.

Chapter three describes the linguliformean fauna of the Deadwood Formation from the subsurface of Alberta and Saskatchewan, which consisted of twelve species assigned to eight genera, and included two new species. A new subfamily, Neotretinae is also erected. Several of the species described are characterstic of faunas from Australia and Kazakhstan, demonstrating the cosmopolitan nature of some linugliformean species. This study was undertaken at the request of the Geological Survey of Canada in order to determine an age for the Deadwood Formation in Canada, which was previously unknown since the only other fossils present are a sparse, non-diagnostic conodont fauana. Based on the linguliformean fossils, the studied interval from the Alberta subsurface was determined to be late Marjuman (early Late Cambrian) in age, while the

interval from the Saskatchewan subsurface was late Steptoean to early Sunwaptan (middle Late Cambrian) in age. These are the first reliable dates for any part of the Deadwood Formation in Canada and demonstrate the potential usefulness of linguliformean brachiopods for biostratigraphy.

Chapter four describes the fauna from the Deadwood Formation from the Black Hills of South Dakota, which consisted of thirty-six species assigned to twenty-three genera, and included fifteen new species, five new genera. A new family, Holmerellidae is also erected. The South Dakota fauna is contemporary with that of the Alberta fauna and is also late Marjuman in age, and corresponds to the *Cedarina dakotaensis* zone found in the lowermost part of the Deadwood Formation in South Dakota. Many of the species described in this chapter are shared in common with Australia and Kazakhstan, and further illustrates the cosmopolitan nature of lingulifomeans. It also suggests a faunal connection between these three regions, and a hypothetical circulation map for the Late Cambrian is proposed to account for the distribution of these taxa. The map was constructed by modifying present-day gyre cells, while maintaining their pattern of equatorial symmetry, to conform to the continental positions in the Late Cambrian, as they are currently understood.

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PREDATION OF LATE CAMBRIAN LINGULIFORMEAN BRACHIOPODS FROM THE DEADWOOD FORMATION OF SOUTH DAKOTA

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Abstract

One hundred and forty linguliformean brachiopods of Late Cambrian age with shell perforations, presumably caused by predation, were recovered from two localities of the Deadwood Formation in the Black Hills of South Dakota, and include the first reported evidence of predation of fossil lingulids. Two types of perforations are attributed to the work of predators: round holes with a sharp, non-beveled exterior edge, and irregularly shaped holes with chipped interior edges. The former type of hole is attributed to either steady pressure applied over a period of time (e.g. boring) or a swift piercing percussive strike, while the latter is attributed to a smashing percussive strike with a blunt appendage to break the shell. A third type of perforation consisting of minute, roughly circular holes is thought to be too small to be the work of predators, and is assumed to be the result of either an encrusting organism or one mining the shell for minerals.

Various hypothetical predators are suggested as potential candidates for causing the shell perforations. The criteria for their selection as possible linguliformean-predators include possessing the ability to produce one of the two types of shell perforation, and being small enough to warrant preying upon one to two millimetre sized brachiopods.

Introduction

Fossil evidence of predation, particularly in the Cambrian, is sparse and limited to shell perforations and breakages, coprolites and trace fossils, although borings in shells of *Cloudina* extends the fossil record of predation back to the latest Neoproterozoic (Bengtson and Yue, 1992; Hua et al., 2003). Cambrian prey taxa, for which direct fossil evidence of predation exists, are those of linguliformean brachiopods (e.g. Miller & Sundberg, 1984; Chatterton & Whitehead, 1987; Conway Morris & Bengtson, 1994) and trilobites (e.g. Alpert & Moore, 1975; Conway Morris & Jenkins, 1985; Pratt, 1998).

Typically, the predators responsible for shell damage to prey species have been left unspecified, but the variety of Cambrian predators, as found in soft-bodied faunal localities such as the Burgess Shale, allow us to infer the types of animals that might have been capable of producing the evidenced damage, and thereby gain a greater understanding of the ecological dynamics of faunal communities in the Cambrian.

Predatory boreholes have been reported in the modern lingulid, *Glottidia* (Paine, 1963; Emig, 1983; Kowalewski & Flessa, 1994), and were attributed to an unspecified boring organism that produced circular drill holes, which were countersunk in some, but not all, specimens. None have been reported from fossil lingulids, and even among modern specimens boreholes are very rare, occurring, for example, in only one valve out of 1,000 specimens collected by Kowalewski and Flessa (1994). The paucity of boreholes in lingulids is likely due to their mainly infaunal habit, which may have protected them from benthic predators. Acrotretids, on the other hand, lived on the sea floor and relied solely on their shells for protection.

In this paper we describe two types of predatory perforation, present in substantial numbers of specimens of several acrotretid and lingulid species from the Upper Cambrian of South Dakota. These specimens show that, contrary to previous indications, predation on phosphatic brachiopods was a locally significant ecological phenomenon in certain Cambrian settings. We suggest too that each of the perforations was produced by one of three generalized modes of attack.

Geological Setting

The Deadwood Formation is a geographically extensive unit, found in the subsurface of Alberta, Saskatchewan, Manitoba, and north-central USA, and is found in outcrop in South Dakota and Montana, USA. It was deposited in a shallow epeiric sea landward of the passive western margin of Laurentia during the late Middle Cambrian to early Ordovician (Lochman, 1950, 1964a, 1964b) and, although it is geographically situated within the Williston Basin, its deposition predates the origin of the basin.

In South Dakota the Deadwood Formation crops out on the flanks of the Black Hills, dipping away from the centre of the uplift, and unconformably overlies the Precambrian basement. At the type section in Deadwood, South Dakota, as described by Darton (1901), the Deadwood Formation is approximately 125 m thick and consists of a thin interval of basal conglomerate and sandstone, followed by a thick succession of shale, limestone, and pebble-clast conglomerate, which is overlain in turn by a succession of glauconitic sandstone and shale. The Deadwood Formation thickens northward, to a maximum of 270 m near the centre of the Williston basin (Hein & Nowlan, 1998).

Samples were collected from calcareous units in two localities in South Dakota (Fig. 1). Locality A is a 9.3 m thick roadcut of calcareous flat-pebble conglomerate (Fig. 2A). Samples were collected at 1 metre intervals, and the section was only sparsely fossiliferous except at the interval 8 metres from the base, which yielded an extraordinarily abundant linguliformean fauna. Locality B is a 28.2 m thick outcrop at Pole Creek (Fig. 2B). The lower 12 m of the section consists of unfossiliferous quartz arenite, and is overlain by 7.2 m of medium to fine grained sandstone, which displayed valves of the brachiopod *Dicellomus* on some bedding planes. Samples were collected at

1 metre intervals from calcareous beds in the upper 9 m of the section, which yielded an abundant and diverse linguliformean fauana.

Methods

Calcareous samples were dissolved in a 10 percent solution of acetic acid and the resulting residue was washed, sieved, and dried, then examined under low-power magnification. Phosphatic brachiopod valves were picked from the residue using a fine sable brush. Selected specimens of each taxon were mounted on SEM stubs using double-sided tape and sputter-coated with gold, then examined and digitally photographed using scanning electron microscopy.

In their study of predatory borings in the Silurian acrotretid, *Artiotreta*, Chatterton and Whitehead (1987) excluded valves with holes that were not clearly produced by boring organisms, attributing them to post-mortem breakage, but we have included all perforated valves, regardless of the type of hole, because we explore the possibility that a non-boring predator could have produced irregularly shaped holes.

Specimens are housed in the collections of the Department of Paleobiology, National Museum of Natural History (USNM), Smithsonian Institution, Washington, DC.

Discussion

Distribution of perforations

Locality A yielded a total of 1,058 valves, belonging to the orders Acrotretida, Lingulida, and Paterinida, of which 111 showed signs of predation, representing approximately 11 percent of the total (Fig 2A). Locality B yielded 1,143 valves, belonging to the same orders, of which 28 showed signs of predation, representing approximately 2.5 percent of the total (Fig 2B). Perforated valves were separated on the basis of hole shape, the proportion of circular holes to irregular holes, and the proportion of perforated ventral valves to dorsal valves. The total number of dorsal and ventral valves of lingulids and acrotretids is listed in Table 1.

Locality A has, almost exclusively, an acrotretid fauna and the proportions of circular to irregular holes are approximately equal, but there are at least four times as many perforated ventral valves as dorsal valves for both hole types (Fig. 3A). These findings differ from those of Miller and Sundberg (1984), Chatterton and Whitehead (1987), and Conway Morris and Bengtson (1994), all of whom reported a greater incidence of borings in the dorsal valves of acrotretids. Locality B, by contrast, has a predominantly lingulid fauna and there are more than twice as many irregular holes as circular holes and the majority of perforated valves are dorsal (Fig. 3B).

The disproportionate ratio of perforations in one valve over the other in acrotretids could be attributed to relative abundance of dorsal and ventral valves. Chatterton and Whitehead (1987, table 1) recovered nearly twice as many dorsal as ventral valves in their study. Conway Morris and Bengtson (1994, table 1) also recovered approximately twice as many dorsal valves of *Linnarssonia* sp. B as ventral valves.

Likewise, while we found a greater incidence of perforation in acrotretid ventral valves, more than twice as many acrotretid ventral valves than dorsal valves were recovered from locality A. This explanation does not account, however, for the disproportionately high number of perforated lingulid dorsal valves from locality B because there were only half as many dorsal valves as ventral valves recovered from this locality. Conway Morris and Bengtson (1994) suggested that significant selection for one valve over another strengthens the argument that the holes were the result of an attack by a predator.

The percentage of valves with perforations at each stratigraphic horizon (Fig. 2) is a maximum of 12% at locality A, and a maximum of 4% at locality B. The percentage of perforated valves from locality A is significantly higher than the less than 1% of perforated acrotretids reported by Miller and Sundberg (1984), but is consistent with the maximum of 15% percent reported by Conway Morris and Bengtson (1994), and maximum of 10% reported by Chatterton and Whitehead (1987).

Vermeij (1993) noted that the incidence of breakage among shells of shallow water snails varies between 10 and 20 percent in the tropics, but less than 10 percent of shells in the cooler waters of the North Pacific. The incidence of shell breakage at locality A is consistent with the breakage rate among tropical snails, though the incidence of breakage is considerably less at locality B.

Shape and size of perforations

Two types of perforations are attributed to the work of predators: round holes with a sharp, non-beveled exterior edge (Fig. 4), and irregularly shaped holes with chipped interior edges (Fig. 5). The circular holes ranged from 66 to 130 µm in diameter, with an

average diameter of 107 μm. Most circular perforations had sharp, smooth exterior edges, and none were beveled. Many of the valves had chipped interior edges (e.g. Fig. 4M). Most valves with circular perforations had only a single one, though in one case (Fig. 4O) there were two perforations.

The irregular perforations were generally larger than the circular ones and ranged in size from 137 to 675 μm, measured across the long axis, with an average of 342 μm. The outlines were often jagged (e.g. Fig. 5E, 5M), but in some cases were nearly smooth (e.g. Fig 5D).

Location of perforations

While our specimens do exhibit marked selection for one valve over the other, there appears to be no consistency in the location of the perforations on the valve. Given that the organs of a brachiopod are located in the body cavity in the posterior region of the shell, it could be assumed that boreholes should be located in the umbonal region as the anterior mantle cavity contains only the lophophore and is not as potentially rewarding a location to penetrate the shell. But there are as many valves with perforations in the anterior part of the valve, which open into the mantle cavity. If the perforations described here are the work of predators, this suggests that attacks were located randomly rather than precisely placed.

According to Carricker (1981), little is known about borehole site selection by boring gastropods, but exploration of the shell surface can take between a few minutes to half an hour. During the exploration the proboscis is extended periodically to test the shell surface. It is not known whether there is any consistent preference for a particular

area on the shell, but the gastropods *Urosalpinx cinerea* and *Nucella iapillus* appear to drill boreholes in random locations on most valves. Prosobranchs have a long proboscis, which can be extended deep into the prey to feed upon soft tissues within a wide radius. Therefore, with these predators, precise location of the hole is of little importance.

None of the shells examined showed any evidence of repair to the perforations, which suggests that the perforations were either lethal or were made *post mortem*, for if the brachiopod were still alive another layer of shell material would have been secreted. The ability of acrotretids and lingulids to repair damage has been demonstrated by Holmer (1989, figs. 47L, 50A). Wilson & Palmer (2001) have suggested that some circular boreholes interpreted as predatory may, instead, be domicile exacavations. They referred, specifically, to borings in a cemented crust of valves of the brachiopod, *Onniella meeki,* which Kaplan & Baumiller (2000) had suggested were the work of mixed-motive borers, including predators. The valves were oriented in both concave-up and concave-down positions and, in some cases, boreholes clipped the valve margins. These observations suggest that at least some of the holes were made *post mortem*. The holes in our specimens, however, have chipped margins on the valve interiors, suggesting that penetration was made from the outside. Finally, in most of our specimens, there is only a single hole per valve, which lends support to a predatory hypothesis. We, therefore, conclude that the holes were probably made in live shells, killing the animal.

While it may be argued that only circular boreholes represent undisputable evidence of predation and that irregular holes might be the result of puncture due to agitation by wave action, it is quite possible that there were a variety of predators using various modes of attack that would result in different types of injury, including the

irregularly shaped holes included in this study. Pratt (1998) tested the resistance of hard-boiled egg shells to abrasion by running a strong stream of water over them and agitating them vigorously in coarse-grained sand, and found no evidence of breakage, even after several hours. Similar tests were performed on egg shells with circular holes (described below), and there was no alteration of size or shape of the perforations after such agitation. It is also unlikely that irregular holes could have been made after fossilisation, since the valves are so fragile that they tend to break along areas of weakness or be completely destroyed when even light pressure is applied. We therefore regard the irregular holes as the work of predators and not the result of *post mortem* breakage to either pre- or post-fossilized valves.

Non predatory borings

One lingulid and two acrotretid valves were perforated by microborings (Fig. 6), which are not attributed to the work of a predator. This third type of perforation occurs as frequently as six per valve (Fig 6A) and ranges in size from 20 to 50 μm in diameter, which may be too small to allow effective ingress into the shell. The large number of microborings per valve also suggests a non-predatory origin, but may be the work of a microbial organism.

Modes of attack

In attempting to simulate the types of perforations seen in the linguliformean valves, we envisioned three generalized modes of attack and applied them to the shells of hardboiled eggs to create a variety of holes.

(1) Steady pressure -- a 2 cm finishing nail (Fig. 7A) was placed on the shell and constant, steady pressure was applied until the nail penetrated the shell. The resulting perforations were small and circular, with sharp edges (Fig. 7B). This mode of attack is reflective of a boring-type predator.

(2) Piercing percussive -- a single, sharp blow was made using the 2 cm finishing nail. The resulting hole (Fig. 7C) was similar to that of the above attack mode. The same technique was performed with the narrow end of a set punch (Fig. 7D) and the resulting hole was larger and circular with a sharp edge (Fig. 7E). This mode of attack is that of a piercing thrust with a pointed striker.

(3) Smashing percussive -- Several blows using different parts of the set punch (Fig. 7D) were struck with a swinging rather than a thrusting type of strike. The narrow end created a small, oblong, irregular hole (Fig. 7F). A quick rap with the corner of the head created a medium sized hole with jagged edges (Fig. 7G). Finally, a strong blow with the flat surface of the head created a large irregular hole with jagged edges (Fig. 7H). This mode of attack simulates a swung blow with a blunt striker.

Modern analogues

There are a number of living organisms that utilize the above mentioned attack modes. Examples of a few such modern examples are discussed to provide a model for possible Cambrian predators that might have used similar types of attacks when preying upon lingulate brachiopods.

Gastropods

Every coastal region of the world supports boring gastropods and they can be found at depths ranging from intertidal to greater than 2,700 m, with numbers decreasing in deeper water (Carricker, 1981). Muricacean and naticacean gastropods bore into shells by applying their proboscis to the surface of a shell and scraping away shell material with a radula, often using an accessory boring organ that secretes an enzyme to soften the shell prior to rasping. Muricaceans feed on a wide variety of bivalves, barnacles, gastropods, small crabs, encrusting bryozoans and carrion fish, while naticaceans have a more restricted diet and feed primarily on live bivalves (Carricker, 1981). Many predatory gastropods possess chemoreceptive mechanisms for detecting their prey at a distance.

Muricacean and naticacean boreholes typically possess smooth walls, bevelled edges, and are generally drilled perpendicular to the shell surface. Naticacean boreholes are spherically paraboloid in outline, while muricacean boreholes are more varied in shape (Carricker, 1981). Some nudibranchs also excavate smooth, round, beveled holes, while limpet-like capulids produce asymmetrical, sometimes jagged boreholes. A long proboscis evolved in prosobranchs enabling them to feed on prey that they are not immediately adjacent to. The long proboscis can also be extended deep in to the shell, allowing it to feed on soft tissues in a wide radius. Thus precise location of the borehole is not necessary.

Cephalopods

Some cephalopods, notably octopods, attack shelled prey such as gastropods by boring into the shell using a salivary papilla. Digestive enzymes are secreted through the

borehole and the partially digested tissues are consumed. The boreholes made by cephalopods are asymmetrical and often jagged in shape (Carricker, 1981; Vermeij, 1993).

Nematodes

The Nematoda is the largest of the roundworm phyla, with some 12,000 described species. While many nematodes are parasitic, there are a wide variety of free-living forms found in marine, fresh water, and terrestrial environments. Marine nematodes can be found in all kinds of sediments and at depths ranging from tidal zones to the deepest ocean, and are usually concentrated in the top 5-10 cm (Nicholas, 1984).

There are 87 genera of predatory marine nematodes. They are characterized by a large buccal cavity with powerful teeth or plates in some species, while others contain, in their buccal capsule, a long, lance-like stylet, which extends from the mouth to pierce the prey (Fig. 8) and inject digestive enzymes. Some stylets are hollow and also serve to suck up the digested prey contents (Nicholas, 1984). This type of attack is representative of the piercing percussive attack mode, and would produce a small circular hole (e.g. Fig. 7C).

Stomatopods

Stomatopods, commonly known as “mantis shrimp,” are aggressive crustaceans characterized by a pair of large, raptorial forelimbs, which are adapted for either spearing or smashing prey. Most stomatopods utilize the piercing percussive attack mode to spear their prey, but will make a smashing percussive attack with their dactyl closed when engaged in combat with other stomatopods. Some genera of the Gonodactylidae make a

smashing percussive attack with their dactyl closed when attacking prey with shells or other stomatopods, but will unfold their dactyl to make a piercing percussive attack against soft-bodied prey (Caldwell & Dingle, 1976). This strike is one of the fastest of all known animal movements (Full et al., 1989) and can be completed in as little as 5 milliseconds, even under water (Burrows & Hoyle, 1972; McNeil et al., 1972), generating enormous force relative to the size of the stomatopod. Fossil evidence of predation by stomatopods has been reported in Plio-Pleistocene gastropods (Geary et al., 1991). The holes attributed to stomatopod attack are subcircular to irregular in outline, with sharp edges, and are similar to holes created by the smashing percussive attack mode (Fig. 9F), and to many of the holes found in brachiopod valves from this study.

Full et al. (1989) conducted a study of the prey selection and feeding efficiency of the stomatopod *Gonodactylus bredini* on snails, and found that *G. bredini* (52 mm long) avoided large snails, preferring to attack small and medium-sized targets. The greatest number of snails consumed by *G. bredini* each day were in the smallest size class (2-8 mm), consuming only one third as many snails of the next larger size class (9-16 mm), and only rarely attacking snails larger than 17 mm. Full et al. (1989) concluded that small prey offered the greatest gains for the least amount of time and energy spent.

Humans

Humans are unique in being able to employ all three modes of attack in unarmed combat. Most attacks in martial arts, such as karate, can be attributed to one of the three described attack modes. For example, the steady pressure attack mode is used in joint locks and choke holds. The piercing percussive attack mode is used when performing thrust

punches and in thrusting ‘spearhand’ attacks with the finger tips to penetrate vital areas and pressure points. The smashing percussive attack mode is employed in kicks, knee and elbow strikes, roundhouse punches, and backfist strikes.

A rising elbow strike, employing the smashing percussive attack mode (Fig. 9A), is analogous to the smashing dactyl strike used by Gonodactylid stomatopods, and is effective in shattering hard objects, and is quite capable of breaking bone. Thrusting spearhand attacks, on the other hand, target soft, vulnerable areas such as the solar plexus or throat (Fig. 9B) just as stomatopods make smashing dactyl strikes against armoured targets and spearing attacks against soft-bodied targets.

Possible Cambrian predators of brachiopods

Carricker (1981) pointed out that, except for naticacean gastropods, identification of modern shell-penetrating molluscs based on their boreholes is difficult. To attempt identification of Cambrian predators based on holes would be impossible. It is possible, however, to assemble a list of predators that could potentially have created the shell perforations observed in fossil linguliformeans. The criteria upon which the following organisms are included as potential brachiopod predators are that they are known to have existed in the Middle or Late Cambrian; they employ at least one of the three attack modes described above, and; they are small enough to have been able to perforate and feed upon brachiopods 1-2 mm in size. Unfortunately, very few Cambrian animals are know for certain as predators, and in part the reason for this is that some undoubtedly were soft-bodied and unlikely to be fossilized.

Yohoia

As noted by Pratt (1998), the Burgess Shale arthropod, *Yohoia tenuis* Walcott, 1912, bears a resemblance to modern stomatopods and may have employed a similar method of attacking prey. Based on the reconstructions of Whittington (1974), the distal segment of the great appendage appears to be robust, particularly around the joint, and may have been well armoured, albeit not heavily calcified. The reinforced distal segment may have been used for striking in a manner similar to the dactyl strike of stomatopods and the elbow strike, used in karate, against hard surfaces (Fig. 10). The great appendages of *Yohoia* bear four distal spines, which Whittington (1974) suggested might have been used to transport food to the mouth. Assuming a smashing attack mode using the thickened distal segment of the great appendage, these spines would, indeed, have been useful for removing soft tissue from within the brachiopod shell and carrying it to the mouth. Though Whittington (1974) did not believe that the spines served any function as cutting or crushing devices, it is conceivable that they could have been held close together for striking at soft-bodied prey, much as human fingers are employed in spear hand strikes.

Yohoia tenuis ranges from 7 to 23 mm in length, which is a suitable size for preying upon linguliformeans. Even individuals at the upper end of the size range might have done so if they had the same preferences for prey selection as stomatopods do, which would have been likely if the optimal feeding efficiency achieved by attacking small prey was also true of Cambrian predator-prey dynamics.

Monoplacophorans

Monoplacophorans are primitive limpet-shaped or spiral-shelled molluscs, and the group is thought to be ancestral to the Gastropoda. Though they are uncommon today, represented by only about 10 species, they are common Cambrian fossils, first appearing in the Lower Cambrian. Extant monoplacophorans have radulae similar to those of a gastropods that possess them. Although living species have long, coiled intestines, typical of herbivores or deposit feeders (Runnegar, 1987), little is known about the palaeobiology of fossil forms. Many of the boreholes in the linguliformean valves are subcircular to slightly elliptical, which is reminiscent of holes made by many gastropods. Though none of the boreholes observed are bevelled, a feature characteristic of most gastropod boreholes, it is not a necessary feature of radular boring. Of approximately 30 Middle Ordovician acrotretid valves described by Holmer (1989), with boreholes attributed to predation by an unknown animal, some had countersunk margins, while others did not.

Conclusions

The high incidence of perforations of acrotretid ventral valves suggests that they may have been preyed upon by small, benthic predators, since the ventral valve is closest to the substrate and, therefore, easier to access.

Many lingulids are infaunal, dwelling in vertical burrows in soft sediment. Perforations in lingulid valves, particularly when located in the posterior region of the valve, if predatory in origin, would imply an infaunal predator, such as a nematode-like organism. The infaunal habit of many lingulids might also explain why little evidence of predation has ever been reported in this group, since by dwelling in burrows the lingulids were likely safe from most benthic predators. It would also explain the below average rate of predation seen in specimens from locality B. Circular holes in lingulid valves were likely caused by a percussive piercing attack, such as could be made by the piercing stylet of a carnivorous nematode, rather than by boring, as any known boring organism would have difficulty accessing the lingulid in its burrow. Though there is no fossil evidence of nematodes in the Cambrian, it is not unreasonable to assume that they, or another animal sharing a similar lifestyle, might have existed.

More problematic are large, irregular perforations in lingulid valves (e.g. Fig. 3E). If these perforations are, indeed, predatory in origin, then according to the model presented here, they would have been made by a smashing percussive attack, which would be difficult to perform in the restricted confines of a lingulid burrow. The modern lingulids *Glottidia* and *Lingula* are, on occasion, removed from their burrows necessitating that they reburrow, and Emig et al. (1978) suggested that fossil U-shaped burrows could be made by lingulids reburrowing after displacement, which implies that

lingulids were able to burrow in the past as well. While exposed on the surface, the lingulid is vulnerable to predation (Emig, 2000), and an epifaunal predator could have inflicted the large irregular perforations upon brachiopods in such a situation.

It is apparent that there was more than one type of predator, and perhaps several, preying upon linguliformean brachiopods in the Late Cambrian. Although predators cannot be identified based on the nature of their perforations, the model for attack modes discussed here provides a framework in which to consider a suite of such predators that could be capable of producing such perforations.

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Fig. 1. Map of study area in the Black Hills of South Dakota. Locality A is a roadcut on highway 385 south of Deadwood. Locality 'B' is an outcrop located next to a logging road at Pole Creek, approximately 15 km southwest of Deadwood.

Fig. 2. Stratigraphic distribution of linguliformean brachiopods and percentage of population with perforated valves. A. Distribution at locality A, a 9.3 m thick unit of flat-pebble limestone conglomerate. B. Distribution at locality B. Unit 1: massive-bedded quartz arenite. Unit 2: thin to medium beds of medium-grained sandstone interbedded with thin beds of fine-grained glauconitic sandstone. Unit 3: fine-grained sandstone. Unit 4: interbedded shale and limestone conglomerate. Unit 5: interbedded shale and lenticular sandstone. B.

Fig. 3. Graphs showing the number of perforated ventral and dorsal valves of each hole type at A. locality A. B. locality B.

Fig. 4. Linguliformean brachiopod valves with circular holes. A. Lingulida gen. et sp. indet. dorsal exterior; USNM 527238, x30. B. Enlargement of A, x185. C. Lingulida gen. et sp. indet. dorsal exterior; USNM 527239, x25. D. Enlargement of C, x150. E. Zhanatellidae gen. et. sp. nov. ventral exterior; USNM 527240, x15. F. Enlargement of E, x60. G. Zhanatellidae gen. et sp. nov. ventral exterior; USNM 527241, x25. H. Enlargement of G, x225. I. Obolidae gen. et. sp. indet. dorsal exterior; USNM 527242, x20. J. Enlargement of I, x110. K. *Canthylotreta* n. sp. ventral exterior; USNM 527245, x45. L. Linnarssoniinae gen. et sp. nov. ventral interior; USNM 527244, x45. M. Enlargement of L, x205.

Fig. 5. Linguliformean brachiopod valves with irregular holes. A. Zhanatellidae gen. et. sp. indet. dorsal exterior; USNM 527246, x18. B. Enlargement of A, x160. C. Lingulida gen. et sp. indet. dorsal exterior; USNM 527247, x35. D. Enlargement of C, x210. E. Zhanatellidae gen. et sp. indet. dorsal exterior; USNM 527248, x10. F. Enlargement of E, x40. G. Enlargement of E, x18. H. Enlargement of G, x260. I. Enlargement of G, x290. J. *Kotylotreta* n. sp. dorsal exterior; USNM 527249, x18. K. Enlargement of J, x55. L. *Canthylotreta* n. sp. dorsal exterior; USNM 527250, x20. M. *Canthylotreta* n. sp. ventral interior; USNM 527251, x25. N. Linnarssoniinae gen. et sp. nov. dorsal interior; USNM 527252, x16. O. *Canthylotreta* n. sp. ventral exterior; USNM 527253, x16. P. Enlargement of O, x90.

Fig. 6. Linguliformean brachiopod valves with microborings. A. Zhanatellidae gen. et sp. indet. dorsal exterior; USNM 527254, x10. B. *Canthylotreta* n. sp. ventral exterior; USNM 527243, x115. C. *Canthylotreta* n. sp. ventral exterior; USNM 527255, x20.

Fig. 7. Circular holes in hard-boiled egg shells. A. 2 cm finishing nail used to make holes B and C. B. Small circular hole made by applying steady pressure with finishing nail (A). C. Small Circular hole made by striking shell with pointed end of finishing nail (A). D.

Set punch used to make holes E-H. E. Large circular hole made by striking shell with pointed end of set punch (D). F. Small sized irregular hole made by striking shell with pointed end of set punch (D) using a swung blow. G. Medium sized irregular hole made by striking shell with corner of blunt end of set punch (D). H. Large sized irregular hole made by striking shell with flat blunt end of set punch (D).

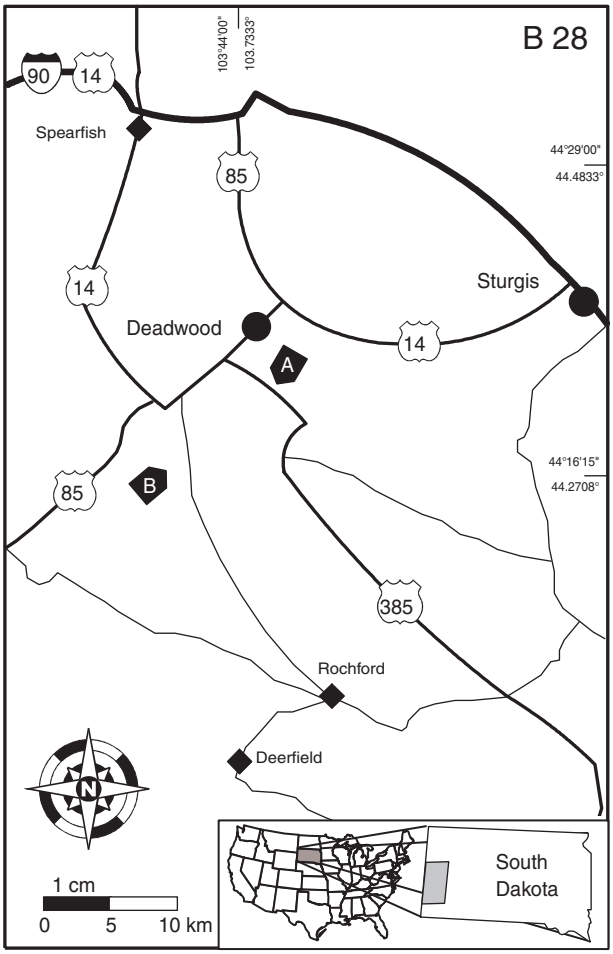
Fig. 8. Generalized diagram of a predatory nematode. A. Piercing stylet withdrawn into sheath. B. Piercing stylet extended through mouth.

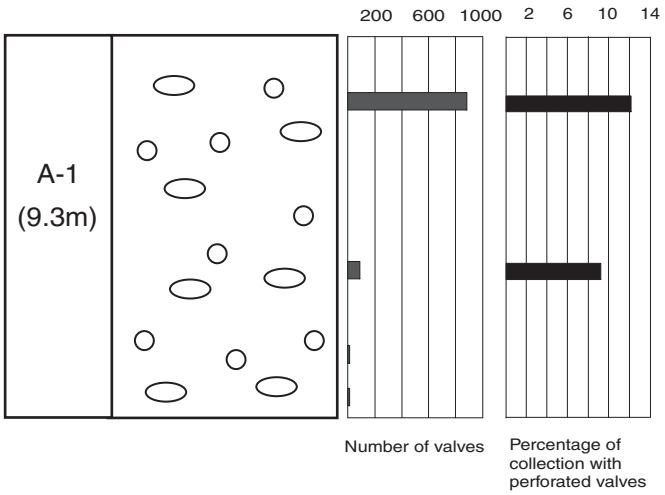
Fig. 9. Sensei Jerry Marr demonstrates techniques on opponent, Eugene Fillion. A. *Age empi uchi* (rising elbow strike) to opponent's chin. B. *Nukite* (spear hand strike) to opponent's throat.

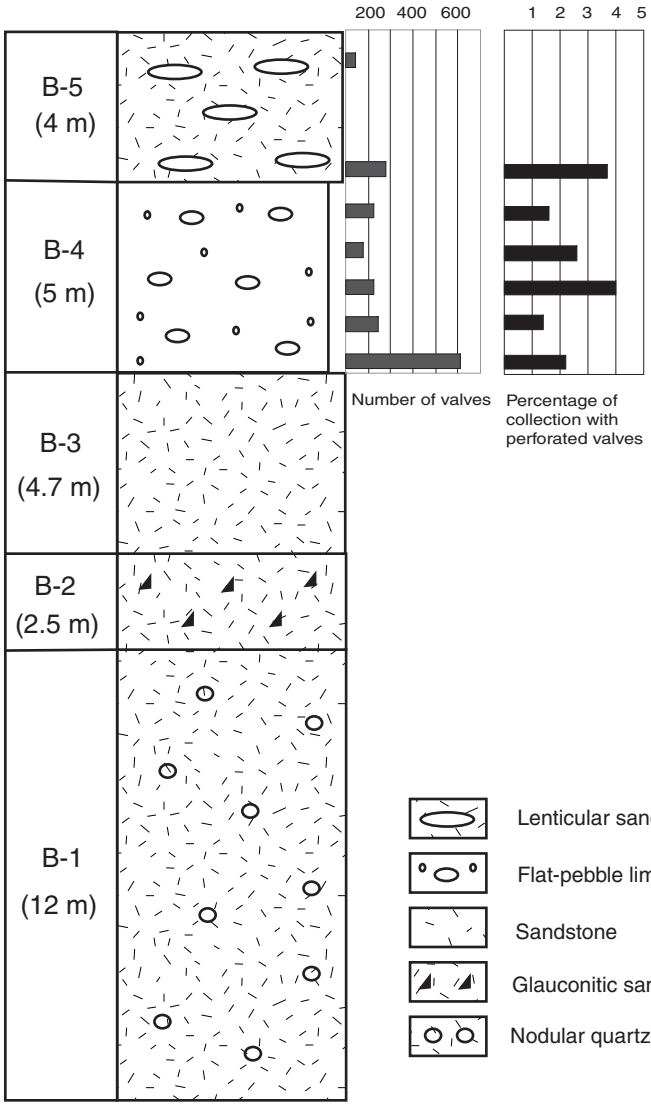
Fig. 10. Diagram of limbs of a gonodactylid stomatopod and of *Yohoia tenuis* in open position (A) and folded position for smashing percussive strike (B).

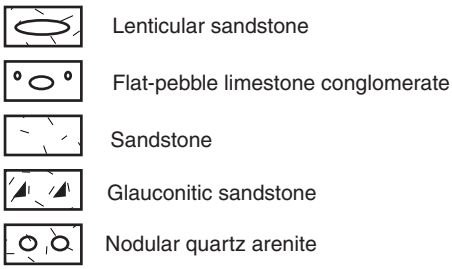
Table 1. Numbers of ventral and dorsal valves of acrotretid and lingulid brachiopods with shell perforations attributed to predation, recovered from localities A, and B.

	Locality ‘A’		Locality ‘B’	
	Ventral valves	Dorsal valves	Ventral valves	Dorsal valves
Lingulida	3	10	421	216
Acrotretida	561	276	97	87

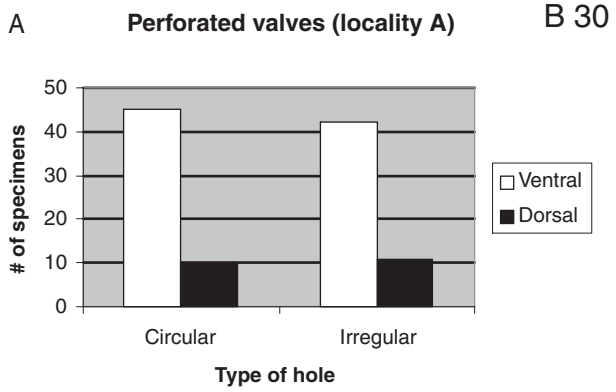

B 28
103°44'00"
103.7333°
90
14
Spearfish
85
44°29'00"
44.4833°
14
Sturgis
Deadwood
14
A
85
B
44°16'15"
44.2708°
385
Rochford
Deerfield
N
1 cm
0 5 10 km
South Dakota


200 600 1000
2 6 10 14
A-1
(9.3m)
Number of valves
Percentage of collection with perforated valves

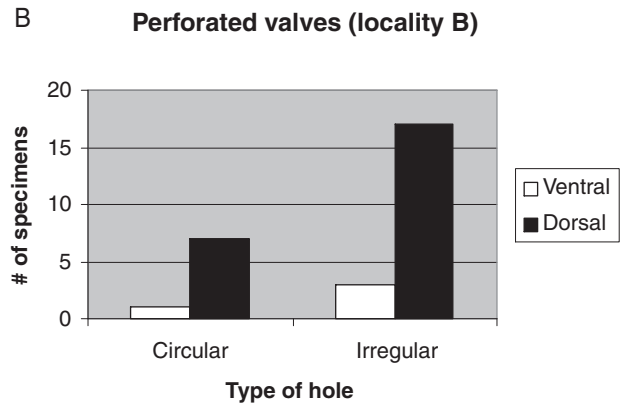

200 400 600
1 2 3 4 5
B-5
(4 m)
B-4
(5 m)
B-3
(4.7 m)
B-2
(2.5 m)
B-1
(12 m)
Number of valves
Percentage of collection with perforated valves

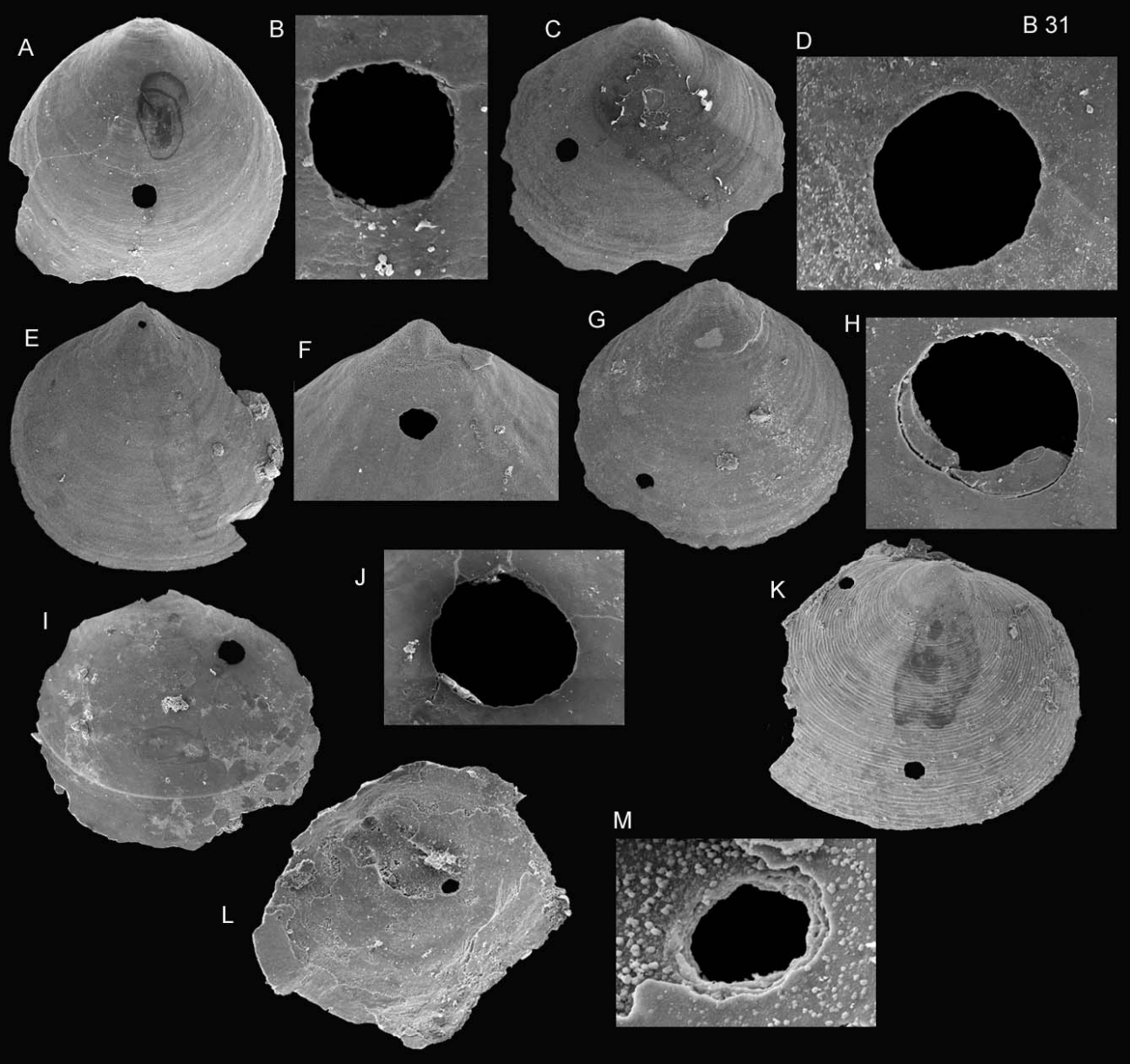

Lenticular sandstone
Flat-pebble limestone conglomerate
Sandstone
Glauconitic sandstone
Nodular quartz arenite

A


Perforated valves (locality A)
50
40
30
20
10
0
# of specimens
Ventral
Dorsal
Circular
Irregular
Type of hole

B


Perforated valves (locality B)
20
15
10
5
0
# of specimens
Ventral
Dorsal
Circular
Irregular
Type of hole


A
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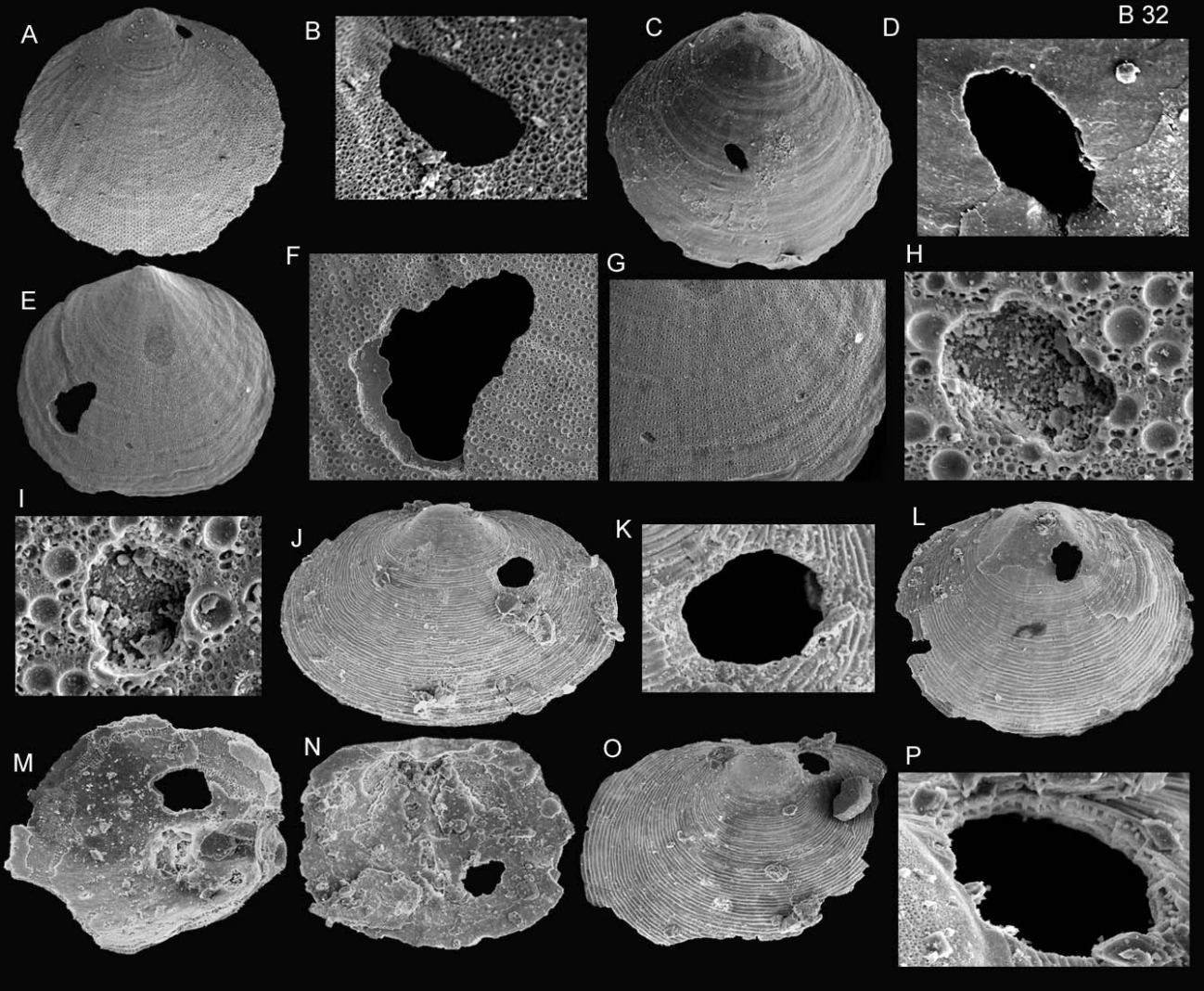
M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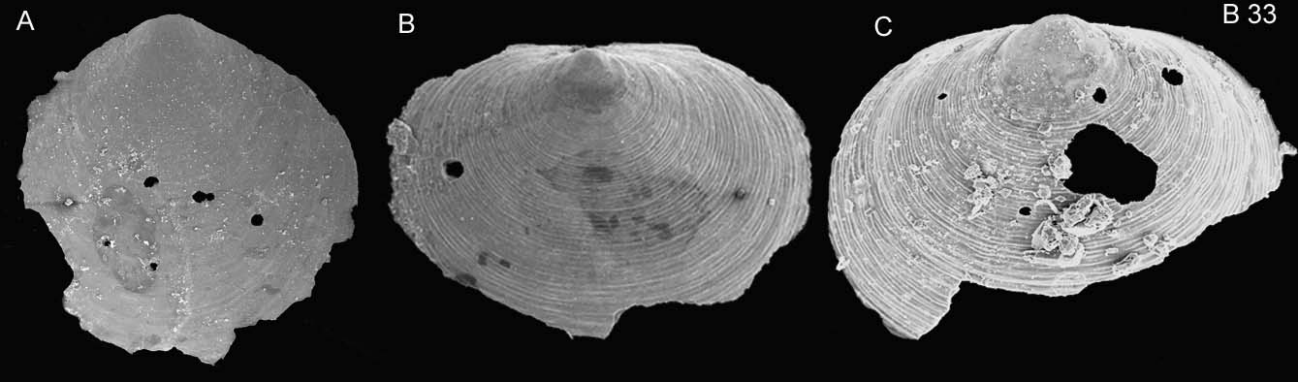
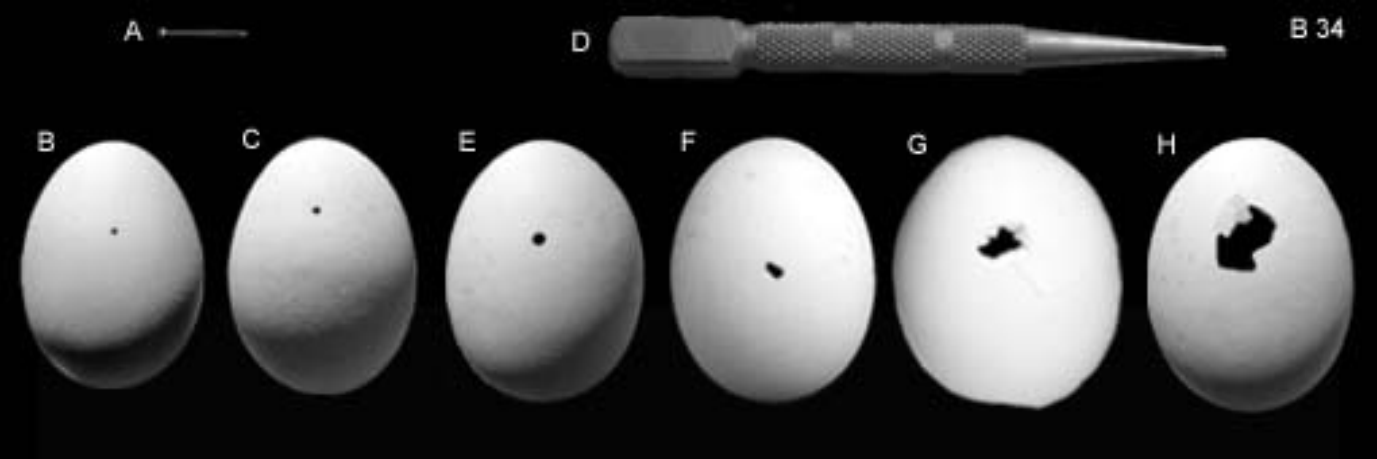
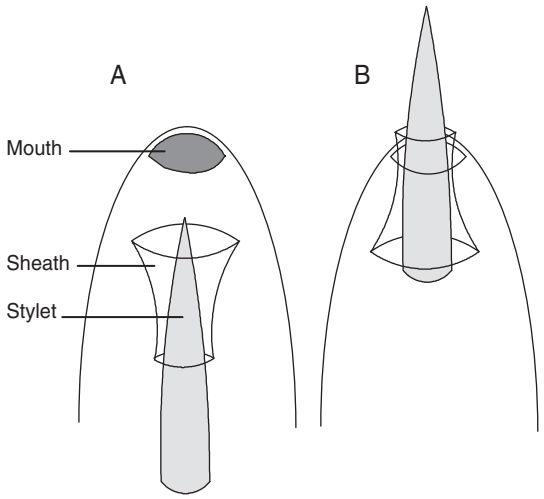
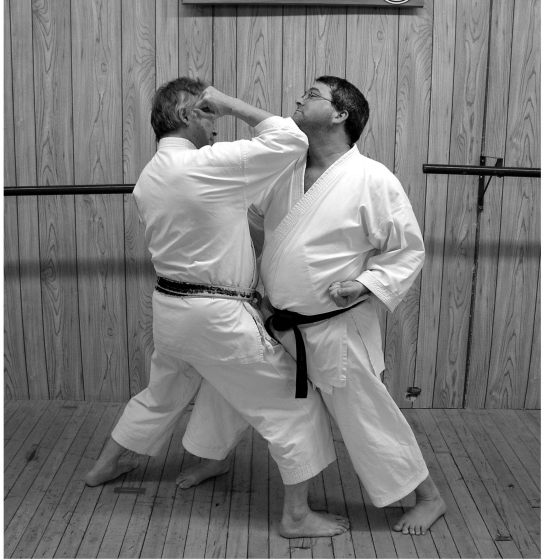

A
B
C
B 33


A
D
B 34
B
C
E
F
G
H

B 35

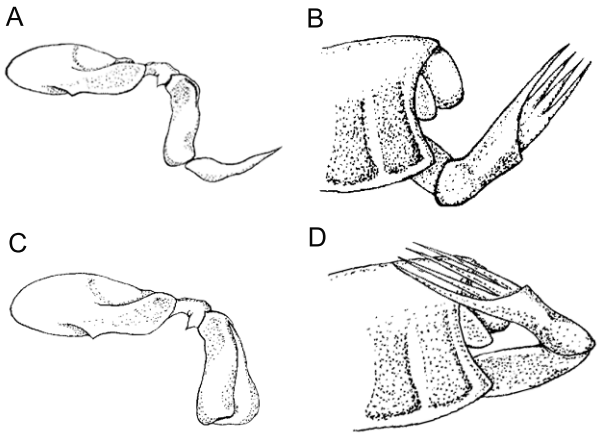


A



B

B 37



MIDDLE TO UPPER CAMBRIAN LINGULIFORMEAN BRACHIOPODS FROM THE DEADWOOD FORMATION OF SUBSURFACE ALBERTA AND SASKATCHEWAN, CANADA

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ABSTRACT--Limestone beds intercalated within a succession of sandstones, siltstones, and shales of the subsurface Deadwood Formation, cored in two wells in Alberta and Saskatchewan, yielded twelve species assigned to eight genera of organophosphatic brachiopods (Subphylum Linguliformea). The nine species recovered from the Alberta

well are Marjuman (late Middle to early Late Cambrian) in age. Three of these species, Neotreta davidi Popov, Berg-Madsen, and Holmer, 1994; Picnotreta debilis Henderson and MacKinnon, 1981; and Stilpnotreta magna Henderson and MacKinnon, 1981, are associated with the Mindyallan (early Late Cambrian) of Queensland, and are previously unknown from Laurentia. This brachiopod fauna occurs with a diverse fauna of paraconodont species. The Saskatchewan well yielded three species of Linnarssonella, belonging to the upper Steptoean to the lower Sunwaptan (middle Late Cambrian). One new subfamily, Neotretinae, is erected, and two new species, Rhondellina albertensis, and Linnarssonella tubicula are described. Linnarssonella elongata Bell, 1941, is reinstated as a valid species. This fauna occurs with a diverse fauna of paraconodont species and is overlain, 226 feet higher, by conodonts of the Early Sunwaptan Proconodontus Zone.

INTRODUCTION

LINGULIFORM BRACHIOPODS are common elements of many Lower Paleozoic marine faunas but are relatively understudied compared to other fossil groups, especially trilobites. Many Cambrian units in which these brachiopods are abundant have yet to be studied with a view to realizing their biostratigraphic and biogeographic potential. Aided by recent refinement of brachiopod systematics (Williams et al., 1996), and increasingly refined trilobite biozonations with which to correlate, linguliform brachiopods are becoming increasingly important biostratigraphic indicators, particularly in units that lack trilobites.

The Deadwood Formation was deposited in a shallow intracontinental sea shoreward of the passive margin of western Laurentia (Hein and Nowlan, 1998) and in

western Canada is known only from sparsely fossiliferous core samples. Linguliform brachiopods have been reported from the Williston Basin in Montana (Bell, 1941, 1944; Lochman, 1964a, 1964b), but not in western Canada. While core samples taken from wells in Alberta and Saskatchewan (Fig. 1) were devoid of trilobites, acetic acid etching yielded a conodont fauna and an abundant, well-preserved organophosphatic brachiopod fauna. The specimens described in this study are the first documented Cambrian brachiopods from the subsurface in western Canada. Three of the species from the Alberta subsurface are previously unknown from Laurentia, and demonstrate that some species of brachiopods are more cosmopolitan than previously believed.

LOCALITIES

The brachiopods reported herein were encountered in etched residues of samples processed for conodonts. The Alberta locality is the Alberta Farrow Well located at 10-11-20-24W4; this well formed part of a study of the Cambrian and Lower Ordovician in the Alberta part of the Western Canada Sedimentary Basin (Hein and Nowlan, 1998). This well is in the southern part of the region where the Deadwood is thin and comprises interbedded sandstone, shale, and limestone (see Hein and Nowlan, 1998, Pl. 1). Nine samples from Alberta Farrow yielded both conodonts (Hein and Nowlan, 1998) and the brachiopods reported herein. The Saskatchewan locality is the Ceepee Reward Well located at 4-28-38-24W3; two samples from this well yielded both conodonts and brachiopods. The conodont data from this well forms part of a continuing study of the Deadwood Formation in Saskatchewan and is not formally published but is the subject of

an unpublished report available from the Geological Survey of Canada (Nowlan, 1999). All well depths are cited in feet because the wells were originally logged in feet.

BIOSTRATIGRAPHY AND BIOGEOGRAPHY

Alberta Farrow Well.--Eight species of brachiopods were collected from a thirty-six foot interval of the core (Fig. 2). Micromitra modesta, known to range from the Middle to Upper Cambrian, was recovered from the bottom of the interval. Neotreta davidi and Stilpnotreta magna first appear six feet above the bottom of the interval, and are previously unknown from Laurentia. Neotreta davidi was previously known only from the lower Upper Cambrian (Mindyallan) Mungerebar Limestone of western Queensland (Popov et al., 1994). Picnotreta debilis, was previously known only from the upper Middle to lower Upper Cambrian (Boomerangian to Mindayallan stages) of western Queensland and New Zealand (Henderson and MacKinnon, 1981). Picnotreta cf. robusta was recovered from a single horizon in the interval. Picnotreta robusta is known only from the lower Los Sombreros Formation of the Argentinean Precordillera (Holmer, et al., 1999), and from the Marjuman of the Shallow Bay Formation in western Newfoundland (Robson and Pratt, 2001). Stilpnotreta magna was previously known from the upper Middle to lower Upper Cambrian (Boomerangia to Mindyallan stages) of western Queensland and New Zealand, and from the Middle Cambrian of Kazakhstan. In addition, Angulotreta is a predominantly Upper Cambrian genus; Opisthotreta ranges from Middle to Upper Cambrian; and Rhondellina is known from the Marjuman of the United States, Canada, and North Greenland; and from the Ayusokkan stage (Middle to Upper Cambrian) of Kazakhstan (Holmer et al., 2001).

The co-occurrence of these brachiopods shows that the fossiliferous interval of the Alberta Farrow Well is Marjuman in age, and that some linguliformean species are very cosmopolitan in their distribution.

Ludvigsen and Westrop (1985) defined the base of the Marjuman as the base of the Ptychagnostus atavus Zone and its top as the base of the Aphelaspis Zone, and considered it to be the base of an expanded Upper Cambrian series. This bipartite division of the Cambrian was not widely accepted, and Palmer (1998) proposed a new regional nomenclature for Cambrian stages and series in North America, and assigned the Marjuman Stage to the upper Lincolnian Series, which extends from upper Middle to lower Upper Cambrian. Traditionally, the base of the Upper Cambrian in North America has been defined as the base of the Cedaria Zone, which placed it in the upper Marjuman. The Cambrian System lacks internationally recognized series and stages, and thus depends entirely on regional stadial schemes. The position of the Upper Cambrian boundary, in particular, is ambiguous and is presently under discussion by the International Subcommission on Cambrian Stratigraphy (Geyer and Shergold, 2000). The brachiopod fauna described from the Alberta Farrow Well occurs within the upper Marjuman stage, and corresponds with the brachiopod fauna of the Mindyallan (upper Middle to lower Upper Cambrian). The fauna also correlates with trilobites from the lower part (Crepicephalus Zone) of the Deadwood Formation in the Black Hills of South Dakota described by Stitt and Perfetta (2000). This suggests that the upper Marjuman, at least, extends into the Upper Cambrian.

The conodonts from this well have been reported by Hein and Nowlan (1998). The fauna, which includes a wide variety of paraconodont species belonging to

Furnishina (Müller, 1959), Muellerodus (Miller, 1980), Phakelodus (Miller, 1984), and Westergaardodina (Müller, 1959), was assigned to an informal "paraconodont zone" that regionally underlies Late Cambrian (Sunwaptan) euconodont faunas that include representatives of Proconodontus (Miller, 1969) and Eoconodontus (Miller, 1980). The earliest euconodont, Proconodontus, first appears in equivalents of the Ellipsocephaloides Trilobite Zone (early Sunwaptan) (see Miller, 1988). However, no euconodonts were recovered from the Alberta Farrow Well and its age could not be constrained because of the lack of a zonation for the Middle and early Late Cambrian paraconodont faunas for North America. The assignment of a Marjuman age based on the brachiopods enhances our understanding of this part of the Cambrian in the subsurface of Alberta.

Ceepee Reward Well.--Three species of the Upper Cambrian genus Linnarssonella were recovered. Linnarssonella girtyi and Linnarssonella elongata were found in two collections over a five-foot interval, whereas Linnarssonella tubicula n. sp. was found only from a single horizon at the base of this interval (Fig. 2). Linnarssonella elongata was first described by Bell (1941) from the Upper Cambrian Dry Creek Shale, and Snowy Range Formation of Montana. It commonly co-occurs with Linnarssonella girtyi, and due to its lack of stratigraphic or geographic distinctiveness, Bell, in Bell and Ellinwood, (1962) reevaluated its validity as a species, considering it to be a morphotype of L. girtyi. Lochman (1964a) subsequently reported Linnarssonella elongata from the Upper Cambrian of the Deadwood Formation of Montana. Linnarssonella tubicula n. sp. appears with L. girtyi and L. elongata at the base of the brachiopod-bearing interval of the Ceepee Reward well, but is not found with them in the horizon five feet higher. Linnarssonella most commonly occurs in the Elvinia Zone, as demonstrated by Lochman

(1964a), thus the fossiliferous interval of the Ceepee Reward Well occurs within the uppermost Steptoean to lower Sunwaptan stages.

The conodonts from the Ceepee Reward Well are the subject of an unpublished report (Nowlan, 1999). The samples that produced the brachiopods reported above yielded relatively abundant conodonts. The fauna from the sample at 5214 feet includes Muellerodus cambricus Müller, 1959; Phakelodus tenuis Müller, 1959; and Prooneotodus gallatini Müller, 1959. The fauna from the lower sample (5219 feet) includes Furnishina alata Szaniawski, 1971; F. furnishi Müller, 1959; F. polonica Szaniawski, 1971; Phakelodus tenuis Müller, 1959; Prooneotodus gallatini Müller, 1959; Prosagittodontus eureka Müller, 1959; and P. minimus Müller and Hinz, 1991. These faunas are broadly similar to those from the Alberta Farrow Well, comprising entirely paraconodonts, but they differ at the specific level.

The long core available for the Ceepee Reward Well has permitted sampling through an interval of more than 200 feet. A sample from 226 feet above the highest sample yielding brachiopods (4988 feet) yields a few conodonts assignable to the euconodont genus Proconodontus (Miller, 1969) indicating a Sunwaptan age for the level. This is in good accord with the later age assigned on the basis of brachiopods and will permit better correlation of strata within the Deadwood Formation.

METHODS

Limestone samples were dissolved in 10% acetic acid. Insoluble residues were screened using 200 mesh (75 micron opening) sieves, then separated in tetrabromoethane at specific gravity of 2.85. Conodonts and phosphatic shelled brachiopods were

handpicked from the residue. Brachiopod valves were mounted on SEM stubs, gold-coated and examined and digitally photographed using scanning electron microscopy. Figured specimens are deposited at the Geological Survey of Canada (GSC), Calgary, Alberta, Canada.

SYSTEMATIC PALEONTOLOGY

Class LINGULATA Gorjansky and Popov, 1985

Order ACROTRETIDA Kuhn, 1949

Family ACROTRETIDAE Schuchert, 1893

Subfamily ACROTRETINAE Schuchert, 1893

Genus ANGULOTRETA Palmer, 1954

Type species.--Angulotreta triangularis Palmer, 1954.

Diagnosis.--See Palmer 1954, p. 769.

ANGULOTRETA sp.

Figure 3.1-3.3

Description.--Ventral valve procline with straight posterior margin. Foramen posteriorly directed, enclosed within larval shell. Apical process long, subtriangular, tapering anteriorly.

Material examined.--Two ventral valves from the Alberta Farrow Well. GSC 121537-121538.

Occurrence.--Lower Upper Cambrian (Marjuman), Alberta, Canada.

Genus LINNARSSONELLA Walcott, 1902

Type species.--Linnarssonella girtyi Walcott, 1902.

Diagnosis.--Shell subcircular to elongate oval. Ventral pseudointerarea undivided, apsacline; foramen contained within larval valve; posterolateral margins with ridges; apical process elongate triangular. Dorsal pseudointerarea orthocline to apsacline, with broad median groove; posterolateral margins with deep grooves; median ridge low or absent.

Discussion.--The diagnosis is revised to include an apsacline dorsal pseudointerarea.

LINNARSSONELLA GIRTYI Walcott, 1902

Figure 4.1-4.8

Linnarssonella girtyi WALCOTT, 1902, p. 602; WALCOTT, 1912, p. 666, pl. 78, fig. 5, pl. 79, figs. 1, 1a-1r; LOCHMAN, 1964a, p. 44, pl. 10, figs. 1-11; ROWELL, 1966, p. 17, pl. 2, figs. 19-40; KURTZ, 1971, p. 475, pl. 55, fig. 17.

Diagnosis.--Shell ventribiconvex, subcircular in outline. Incurved beak extends beyond posterior margin. Apical process present as low tube, dorsal surface of tube often absent.

Description.--Ventral valve subcircular in outline with convex posterior margin, and unflattened apsacline pseudointerarea. Incurved beak extends beyond posterior margin, with large, circular, posteriorly to ventrally directed pedicle foramen contained within larval shell. Apical process present as low tube extending anteriorly from pedicle foramen to approximately one quarter of valve length. Muscle scars not preserved. Dorsal valve apsacline with deeply depressed pseudointerarea, and deep grooves on posterolateral margins. Small muscle scars present near posterolateral margins.

Material examined.--Ninety two ventral valves, and one hundred and seven dorsal valves from the Ceepee Reward well, Saskatchewan. GSC 121544, 121545, 121549-121551.

Occurrence.--Upper Cambrian, USA, Canada.

Discussion.-- The ventral valves are similar to those of Linnarssonella girtyi illustrated by Holmer and Popov (2000, fig. 58, 3a-h.).

LINNARSSONELLA ELONGATA Bell,1941

Figure 3.4-3.12

Linnarssonella elongata BELL, 1941, p. 235, pl. 31, figs. 15-19, text figs. 8-10;

LOCHMAN, 1964a, p. 44, pl. 10, figs. 12-19.

Linnarssonella girtyi BELL AND ELLINWOOD, 1962, p. 410, pl. 61.

Diagnosis.--Shell elongate subtriangular in outline. Ventral pseudointerarea strongly apsacline, umbonal region thickened internally, apical process shallowly depressed, bounded by lateral ridges. Pedicle foramen elongate oval, contained within larval valve.

Description.--Shell elongate subtriangular with glossy external surface. Ventral valve nearly as wide as long, maximum width at anterior third of valve. Pseudointerarea apsacline, intertrough convex. Posterolateral margins form elongate, articulatory ridges. Umbo thickened internally, overhanging posterior margin, forming bluntly rounded apex, perforated by elongate oval pedicle foramen. Apical process forms shallow, central depression that broadens anteriorly from pedicle foramen to between one-third and one-half of valve length. Cardinal muscle scars located posterolaterally. Mantle canals not apparent. Dorsal valve with broad, orthocline pseudointerarea; median plate concave;

propareas form deep posterolateral depressions. Median ridge absent. Cardinal muscle scars oval-shaped, located posterolaterally. Mantle canals not apparent.

Discussion.--Bell (1941) distinguished Linnarssonella elongata from L. girtyi on the basis of its elongate, subtriangular outline, bluntly rounded ventral apex, and unflattened ventral pseudointerarea. He later, in Bell and Ellinwood (1962), considered Linnarssonella elongata to be a junior synonym of L. girtyi because he was unable to distinguish any stratigraphic or geographic variation in the two species, and believed it unnecessary to regard it as a separate species solely on these morphological differences. Since then, Linnarssonella girtyi has been generally accepted to have widely variable morphology (Grant, 1965; Rowell, 1966; Kurtz, 1971). As an exception however, Lochman (1964a) reported Linnarssonela elongata from a twelve-foot core interval from the subsurface Deadwood Formation in Montana overlying an eighty-seven foot interval containing L. girtyi, with no co-occurrence of the two forms.

The specimens assigned here to Linnarssonella elongata are identical to those described by Bell (1941), and undoubtedly belong to a discrete taxon exhibiting consistent morphological distinctiveness. It is unlikely for two distinct morphotypes of a single species to occur exclusively at the same time in the same location unless they represent sexual dimorphism. Interbreeding would eliminate the morphological variation in just a few generations, unless the gametes of the two morphotypes matured at different times, which seems unlikely for individuals of the same species in the same community. Because sexual dimorphism is rare in living brachiopods, having been reported in only a single species (Lacaze-Duthiers, 1861), the two morphotypes are considered here to represent separate species.

Material examined.--Fifty three ventral valves and thirty five dorsal valves from the Ceepee Reward Well, Saskatchewan. GSC 121539-121543.

Occurrence.--Upper Cambrian, North America.

LINNARSSONELLA TUBICULA new species

Figure 4.9-4.16

Diagnosis.--Ventral valve with large, circular, posteriorly directed pedicle foramen contained within large larval valve. Elongated ridge extends anteriorly from foramen to approximately two thirds of larval valve length. Dorsal valve with narrow, apsacline pseudointerarea. Median septum absent.

Description.--Shell ventribiconvex, subcircular to transversely suboval in outline, 85 percent as long as wide. Ventral valve apsacline, with flattened pseudointerarea. Large, circular, posteriorly directed pedicle foramen contained within relatively large larval valve that overhangs posterior margin. Foramen continues internally as short pedicle tube (Fig. 4.13). Muscle scars not apparent.

Etymology.--Latin, tubus, pipe, diminutive.

Type.--Holotype GSC 121546, Upper Cambrian, Deadwood Formation, Ceepee Reward Well, Saskatchewan.

Other material examined.--Seventeen ventral valves and twenty dorsal valves from the Ceepee Reward Well, Saskatchewan. GSC 121547, 121548.

Occurrence.--Upper Cambrian (Marjuman), Saskatchewan subsurface.

Discussion.--Linnarssonella tubicula is distinguished from other species in having a ventral larval valve that is relatively large for the genus, and a prominent ridge on the

larval valve exterior that likely corresponds to the short internal pedicle tube. The dorsal valve is unique in having an apsacline pseudointerarea, whereas all other species of Linnarssonella have an orthocline pseudointerarea. The dorsal valve possesses the deep grooves on the posterolateral margins, which provide the rudimentary valve articulation characteristic of the genus.

Subfamily LINNARSSONIINAE Rowell, 1965

Genus OPISTHOTRETA Palmer, 1954

Type species.--Opisthotreta depressa Palmer, 1954.

Diagnosis.--See Holmer et al. 1999, p. 234.

OPISTHOTRETA? sp.

Figure 5.13-5.20

Description.--Ventral valve subcircular in outline; posterior margin short, straight. External surface ornamented with fine concentric growth lines. Apical process, muscle scars, mantle canals not apparent. Pseudointerarea apsacline, undivided by intertrough. Foramen large, circular, posteriorly directed, contained within larval shell. Beak present as tubular protrusion of larval valve, extending beyond posterior margin.

Material examined.--Two ventral valves and one juvenile conjoined shell from the Alberta Farrow Well. GSC 121567-121569.

Occurrence.--Upper Cambrian (Marjuman), Alberta subsurface.

Discussion.--The Deadwood specimens are similar to the type species in shell shape and profile, and in lacking an apical process and well-defined muscle scars. They differ, however, in having a flat rather than a concave pseudointerarea, and in having a

tubular projection extending from larval shell. These specimens are also similar in shape to Stilpnotreta magna Henderson and MacKinnon, 1981, but lack the articulatory lip on the pseudointerarea, which is characteristic of Stilpnotreta. The Deadwood specimens likely represent a new species, but due to limited material it is not formally established.

Genus PICNOTRETA Henderson and MacKinnon, 1981

Type species.--Picnotreta debilis Henderson and MacKinnon, 1981.

Diagnosis.--See Robson and Pratt 2001, p. 247.

PICNOTRETA DEBILIS Henderson and MacKinnon, 1981

Figure 6.1-6.3

Picnotreta debilis HENDERSON AND MACKINNON, 1981, figs. 9H-L, O-P, not figs. 9M-N.

Diagnosis.--Ventral pseudointerarea triangular with central convexity, strongly apsacline to catacline. Apical process subtriangular, with narrow, shallow, median concavity. Dorsal valve with poorly developed pseudointerarea.

Description.--Ventral pseudointerarea apsacline with convex intertrough bounded by narrow triangular propareas; buttressed by apical thickening. Apical buttress perforated by pedicle tube, emerging from apex that overhangs posterior valve margin facing in posterior direction. External pedicle foramen confined within larval shell, surrounded by lip. Apical process large, subtriangular, with narrow, acutely subtriangular median concavity. Apical process extends anteriorly from apex to one half of valve length, bounded by long, deeply incised vascula lateralia diverging from apex. Long, lobate cardinal muscle scars located near posterolateral margins of valve.

Material examined.--One ventral valve from the Alberta Farrow Well. GSC 121552.

Occurrence.--Middle to Early Upper Cambrian, Georgina Basin, Queensland; Tasman Formation, New Zealand; and Early Upper Cambrian (Marjuman), Alberta subsurface.

Discussion.--Picnotreta was originally erected as a monospecific genus, and thus the diagnosis for the genus applied to the type species as well. The diagnosis provided here reflects the characters that distinguish Picnotreta debilis from the three other species that have subsequently been described. Picnotreta debilis differs from P. robusta Holmer et al., 1999, P. lophocracenta Robson and Pratt, 2001, and P. karakichiensis Holmer et al., 2001, in having a ventral pseudointerarea with a central convexity and a large, subtriangular apical process with median depression. The ventral pseudointerarea is distinct in being strongly apsacline to catacline, whereas the pseudointerarea of Picnotreta robusta is orthocline, and the pseudointerarea of P. lophocracenta is slightly apsacline to slightly anacline.

PICNOTRETA cf. ROBUSTA Holmer, Popov, and Lehnert, 1999

Figure 6.4, 6.5

cf. Picnotreta robusta HOLMER, POPOV, AND LEHNERT, 1999, p. 236, fig. 9 A-N; ROBSON AND PRATT, 2001, p. 249, figs. 9-10.

Diagnosis.--Ventral valve with subdued apical process, extending anteriorly from triangular buttress of orthocline pseudointerarea to one-half of valve length, surrounded by shallow, U-shaped trough. Dorsal valve with triangular, blade-like median septum, extending nearly entire length of valve.

Description.--Ventral pseudointerarea orthocline, buttressed by apical thickening. Internal foramen medially located on apical process; external foramen on posterior facing beak surrounded by lip formed by concave intertrough. Apical process present as low subtriangular rise extending from buttress to approximately one-half of valve length, surrounded by shallow trough.

Material examined.--Three ventral valves from the Alberta Farrow Well. GSC 121553, 121554.

Occurrence.--Upper Middle to Upper Cambrian, Argentina and western Newfoundland; lower Upper Cambrian (Marjuman), western Canada.

Genus STILPNOTRETA Henderson and MacKinnon, 1981

Type species.--Stilpnotreta magna Henderson and MacKinnon, 1981.

STILPNOTRETA MAGNA Henderson and MacKinnon, 1981

Figure 6.6-6.13

Stilpnotreta magna HENDERSON AND MACKINNON, 1981, p. 298, figs. 7 A-J, 8.

Diagnosis.--Shell biconvex, subcircular in outline. Ventral pseudointerarea apsacline, concave or flat, free margin forms lip. Dorsal pseudointerarea orthocline; median ridge subdued or not apparent. Cardinal muscle scars elongate.

Description.--Shell equally biconvex, subcircular in outline, external surface glossy. Ventral pseudointerarea apsacline, with flat intertrough. Lip on free margin forms articulatory process (fig. 6.13). Thickened apical region perforated by large internal foramen that passes into short tube, emerging as large external foramen. Beak extends only slightly beyond posterior margin. Apical process low subtriangular rise. Cardinal muscle scars elongate. Dorsal pseudointerarea orthocline, with concave

intertrough and narrow, triangular propareas. Subdued median ridge present in posterior third of valve; cardinal muscle scars elongate.

Material examined.--Four ventral valves and one dorsal valve from the Alberta Farrow Well. GSC 121555-121558.

Occurrence.--Middle to lower Upper Cambrian, Georgina Basin, Queensland; Tasman Formation, New Zealand; Middle Cambrian, Kazakhstan; and lower Upper Cambrian (Marjuman), Alberta subsurface.

Subfamily NEOTRETINAE new subfamily

Diagnosis.--Shells small, biconvex, with straight posterior margins and reduced or vestigial pseudointerareas; pedicle foramina contained completely within larval valves.

Discussion.--Rowell (1986) noted that Rhondellina Rowell, 1986, was similar to genera of the Linnarssoniinae, particularly Opisthotreta, in having poorly developed dorsal propareas, but considered it a very derived form due to its shell ultrastructure and morphology of the ventral valve. Likewise, Popov et al. (1994) considered Neotreta to be most closely comparable to Stilpnotreta Henderson and MacKinnon, 1981, due to its strongly biconvex shell and rudimentary pseudointerarea. While Neotreta and Rhondellina do share many features with genera belonging to the Linnarssoniinae, and may have arisen from this group, they seem more closely related to each other than they are to any other genera. The most significant difference between the two genera is that Neotreta has a posteriorly facing pedicle foramen contained within the larval valve with a beak that overhangs the posterior margin, while Rhondellina has a ventrally directed

foramen contained within the larval valve, which only slightly extends beyond the posterior margin of the ventral valve.

Genus NEOTRETA Sobolev, 1976

Type species.--Neotreta tumida Sobolev, 1976.

Diagnosis.--See Popov et al. 1994, p. 346 .

NEOTRETA DAVIDI Popov, Berg-Madsen, and Holmer, 1994

Figure 7.1-7.12

Neotreta davidi POPOV, BERG-MADSEN, AND HOLMER, 1994, p. 353, Fig 5.

Diagnosis.--Shell ventribiconvex, transversely suboval in outline. Ventral pseudointerarea vestigial, forming short strip. Dorsal valve lacking median septum and pseudointerarea.

Description.--Shell ventribiconvex, transversely suboval in outline. Ventral valve strongly convex, approximately 50 percent wider than long. Pseudointerarea catacline, forming short strip. Posterior margin straight, approximately 70 percent of valve width. Apical process low or absent. Oval cardinal muscle scars located near posterolateral margins. Dorsal valve moderately to shallowly convex; pseudointerarea completely reduced; internal features not apparent.

Material examined.--Three ventral valves and three dorsal valves from the Alberta Farrow Well. GSC 121559-121562.

Occurrence.--Upper Cambrian, western Queensland, and Alberta subsurface.

Genus RHONDELLINA Rowell, 1986

Type species.--Rhondellina dorei Rowell, 1986.

Diagnosis.--See Rowell 1986, p. 1059.

RHONDELLINA ALBERTENSIS new species

Figure 5.1-5.7

Diagnosis.--Posterior margin straight, approximately 60 percent of valve width. Apical process absent. Dorsal pseudointerarea absent.

Description.--Shell biconvex, transversely oval in outline, approximately 40 percent wider than long. External surface ornamented with fine, concentric growth lines. Posterior margin straight, approximately 60 percent of valve width. Ventral pseudointerarea vestigial, present as undivided strip. Pedicle foramen large, circular, ventrally directed, contained within larval shell. Shallow groove extends anteriorly from foramen half way to margin of larval shell. Beak of larval valve projects slightly beyond posterior margin. Apical process absent. Posterolateral muscle scars poorly preserved. Dorsal pseudointerarea absent. Larval valve not extending beyond posterior margin. Median septum absent. Posterolateral muscle scars poorly preserved.

Etymology.--Named for the province of Alberta in which the species is found.

Type.--Holotype GSC 121563, Upper Cambrian, Deadwood Formation, Alberta Farrow Well, Alberta.

Other material examined.--One dorsal valve from the Alberta Farrow Well. GSC 121564.

Occurrence.--Upper Cambrian, Alberta subsurface.

Discussion.--Rhondellina albertensis differs from the type species in lacking an apical process, and having a wider posterior margin. It differs from Rhondellina karatauensis Koneva, 1992, in that the latter possesses a bifurcating dorsal median ridge.

Class PATERINATA Williams et al. 1996

Order PATERINIDA Rowell, 1965

Family PATERINIDAE Schuchert, 1893

Genus MICROMITRA Meek, 1873

Type species.--Micromitra sculptilis Meek, 1873.

Diagnosis.--See Laurie 2000, p. 153.

MICROMITRA MODESTA Lochman, 1940

Figure 5.8-5.11

Micromitra modesta LOCHMAN, 1940, p. 14, pl. 1, figs. 20, 21.

Diagnosis.--Delthyrium high, notothyrium short. homeodeltidium and homeochilidium minute.

Description.--Shell subcircular in outline with straight posterior margin, approximately 15 percent wider than long. Interior featureless except for a pair of umbonal depressions corresponding to two callosities on larval valve exterior. Homeodeltidium absent.

Material examined.--One ventral valve from the Alberta Farrow Well. GSC 121565.

Occurrence.--Lower to Upper Cambrian, Missouri, Utah, Monatana, Alberta subsurface, western Newfoundland, and North Greenland.

Discussion.--The specimen illustrated is the ventral valve of a juvenile.

MICROMITRA sp.

Figure 5.12

Description.--Valve fragment ornamented by irregular costae, and non-concentric rugae.

Material examined.--One dorsal valve from the Alberta Farrow Well. GSC 121566.

Occurrence.--Upper Cambrian (Marjuman), Alberta subsurface.

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FIGURE 1--Map of study area showing approximate location of Alberta Farrow (AF) and Ceepee Reward (CR) wells.

FIGURE 2--Stratigraphic distribution of brachiopods in the Alberta Farrow and Ceepee Reward Wells.

FIGURE 3--1-3: Angulotreta sp.; 1, ventral interior, GSC121537, x60; 2,3, ventral valve, GSC121538; 2, posterior view, x195; 3, right lateral view, x180. 4-12: Linnarssonella elongata Bell, 1941; 4,6, ventral valve, GSC121539; 4, ventral interior, x45; 6, internal plan view, x30; 5, interior oblique view, GSC21540, x50; 7,8, ventral valve, GSC121541; 7, external plan view, x40; 8, external posterior view, x60; 9-11, dorsal valve, GSC121542; 9, left lateral view, x50; 10, internal plan view, x55; 11, internal anterior oblique view, x55; 12, dorsal exterior, GSC121543, x35.

FIGURE 4--1-8: Linnarssonella girtyi Walcott, 1902; 1-3, ventral valve, GSC 121544; 1, internal right lateral view, x75; 2, internal anterior view, x90; 3, detail of pedicle foramen, x245; 4, ventral exterior, plan view, GSC 121545, x75; 5,6, dorsal valve, GSC 121570; 5, internal anterior view, x80; 6, internal plan view, x50; 7, dorsal interior, left lateral view, GSC 121571, x80; 8, dorsal exterior, plan view, GSC 121572, x70. 9-16: Linnarssonella tubicula n.sp.; 9, 10, ventral valve, GSC 121546; 9, external plan view, x80; 10, external anterior view, x50; 11, ventral exterior, left lateral view, GSC 121547, x100, 12, 13, ventral valve, GSC 121548; 12, posterior oblique view, x80; 13, internal anterior view, x85; 14, dorsal interior, anterior oblique

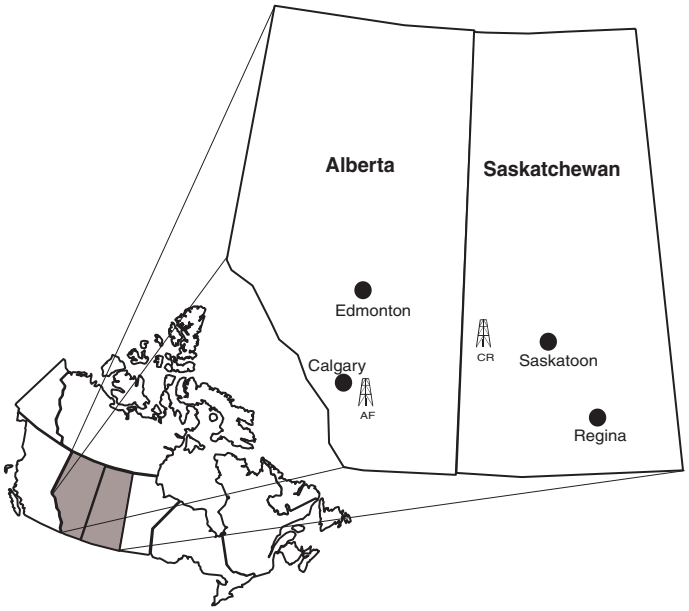
view, GSC 121573, x60; 15, dorsal interior, plan view, GSC 121574, x80; 16, dorsal exterior, plan view, GSC 121549, x80.

FIGURE 5--1-7: Rhondellina albertensis n.sp.; 1-5, ventral valve, GSC121563; 1, external plan view, x110; 2, postero-lateral oblique view, x170; 3, posterior view, x150; 4, internal plan view, x110; 5, detail of posterior margin, x195; 6,7, dorsal valve, GSC121564; 6, external posterior oblique view, x120; 7, internal plan view, x80. 8-11: Micromitra modesta Lochman, 1940, ventral valve, GSC121565; 8, external plan view, x55; 9, anterior view, x65; 10, left lateral view, x65; 11, internal plan view, x60. 12: Micromitra sp., dorsal exterior, plan view, GSC121566, x35. 13-20 Opisthotreta? sp.; 13, 15, 16, ventral valve, GSC121567; 13, postero-internal oblique view, x85; 15, postero-internal oblique view, x115; 16, right lateral view, x160; 14, 17, ventral valve, GSC121568; 14, external plan view, x120; 17, anterior view, x175; 18-20, juvenile shell, GSC121569; 18, right lateral oblique view of ventral valve, x205; postero-lateral view of ventral valve, x190; 20, postero-lateral view of dorsal valve, x 310.

FIGURE 6--1-3: Picnotreta debilis Henderson and MacKinnon, 1981, ventral valve, GSC121552; 1, internal plan view, x75; 2, anterior internal, oblique view, x90; 3, detail of pseudointerarea, x275. 4,5: Picnotreta cf. robusta; 4, ventral valve, right lateral view, GSC121553, x165; 5, ventral valve, antero-lateral oblique view, GSC121554, x175. 6-12 Stilpnotreta magna Henderson and MacKinnon, 1981; 6, ventral valve, internal plan view, GSC121555, x110; 7, 8, dorsal valve, GSC121556; 7, detail of posterior margin, x110; 8, internal plan view, x75; 9, 10, ventral valve, GSC121557; 9, internal anterior, oblique view,

x110; 10, anterior view, x110; 11-13, ventral valve, GSC121558; 11, right lateral view, x230; 12, detail of posterior margin, x300; 13, detail of larval shell, x390.

FIGURE 7--1-12: Neotreta davidi Popov, Berg-Madsen, and Holmer, 1994; 1-7, ventral valve, GSC121559; 1, external plan view, x95; 2, left lateral view, x110; 3, anterior view, x130; 4, internal plan view, x 95; 5, antero-lateral oblique view, x120; 6, left lateral oblique view, x120; 7, anterior oblique view, x120; 8, ventral interior, GSC121560, x195; 9, 12, dorsal valve, GSC121561; 9, external plan view, x145; 12, anterior view, x180; 10, 11, dorsal valve, GSC121562; 10, internal plan view, x110; 11, antero-lateral oblique view, x115.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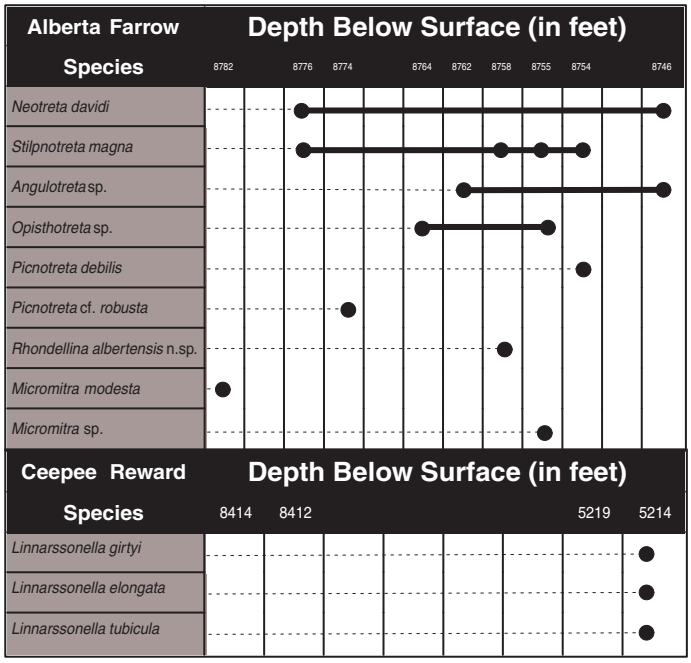
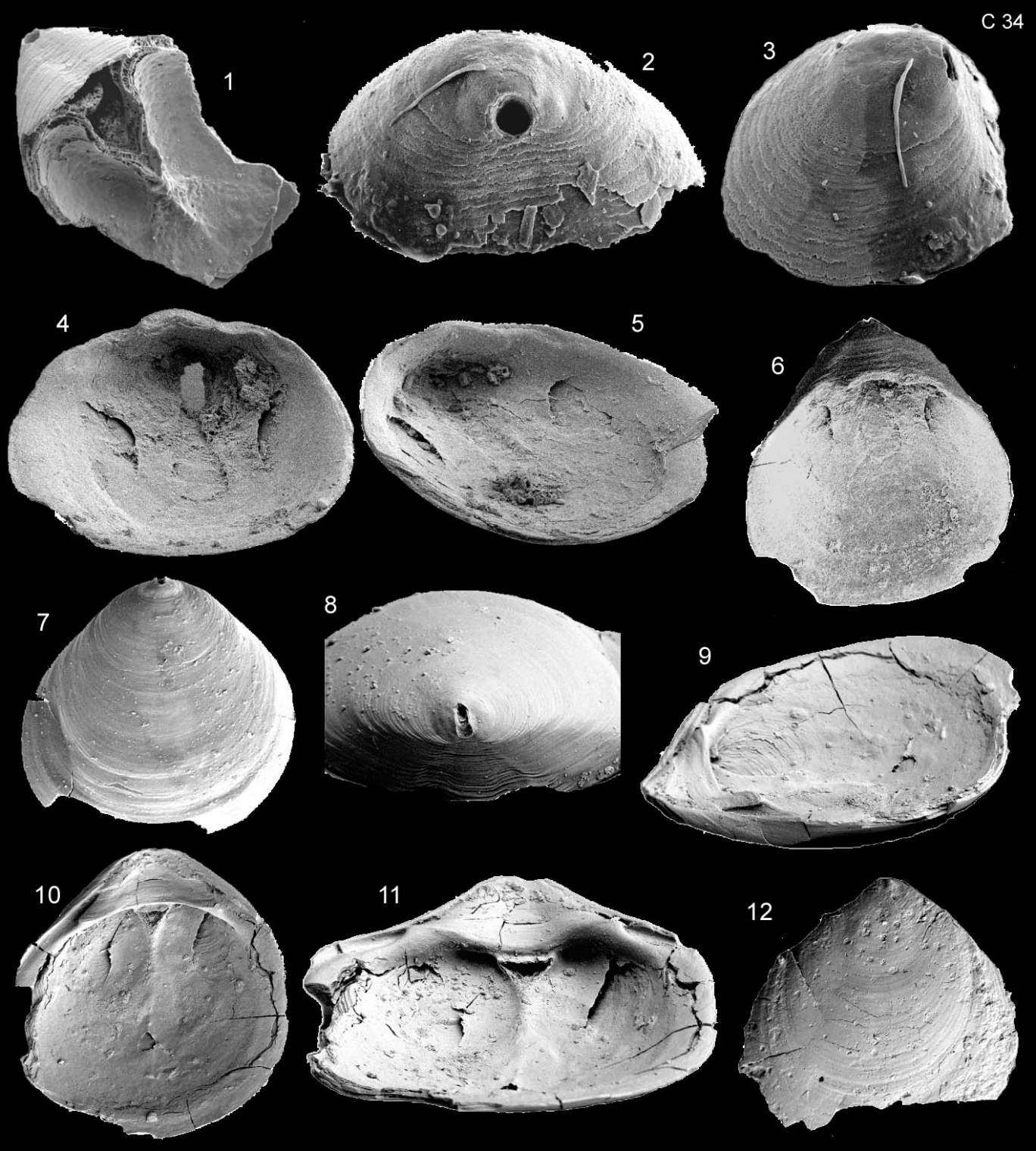

Alberta Farrow
Depth Below Surface (in feet)
Species
8782
8776
8774
8764
8762
8758
8755
8754
8746
Neotreta davidi
Stilpnotreta magna
Angulotreta sp.
Opisthotreta sp.
Picnotreta debilis
Picnotreta cf. robusta
Rhondellina albertensis n.sp.
Micromitra modesta
Micromitra sp.
Ceepee Reward
Depth Below Surface (in feet)
Species
8414
8412
5219
5214
Linnarssonella girtyi
Linnarssonella elongata
Linnarssonella tubicula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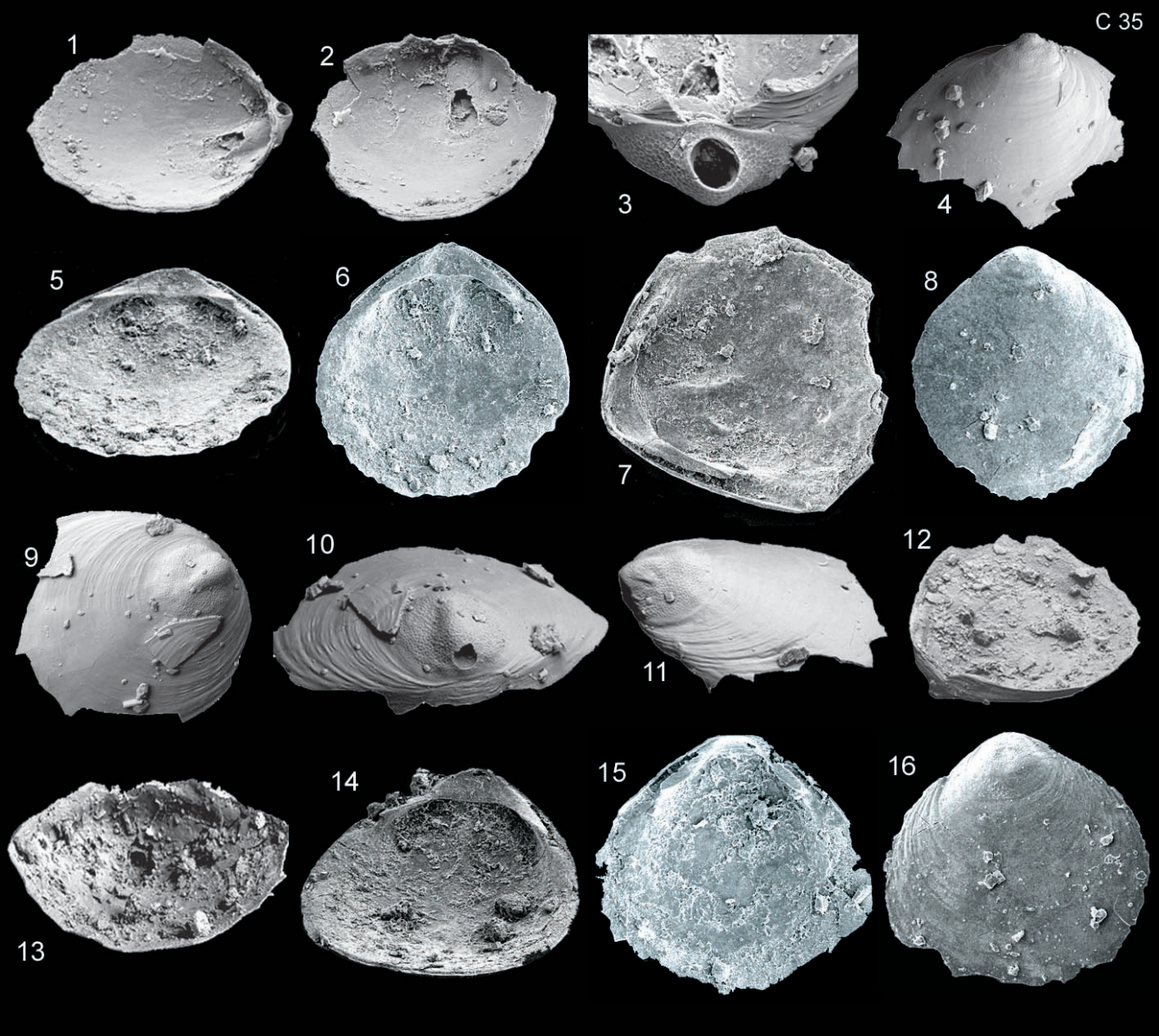
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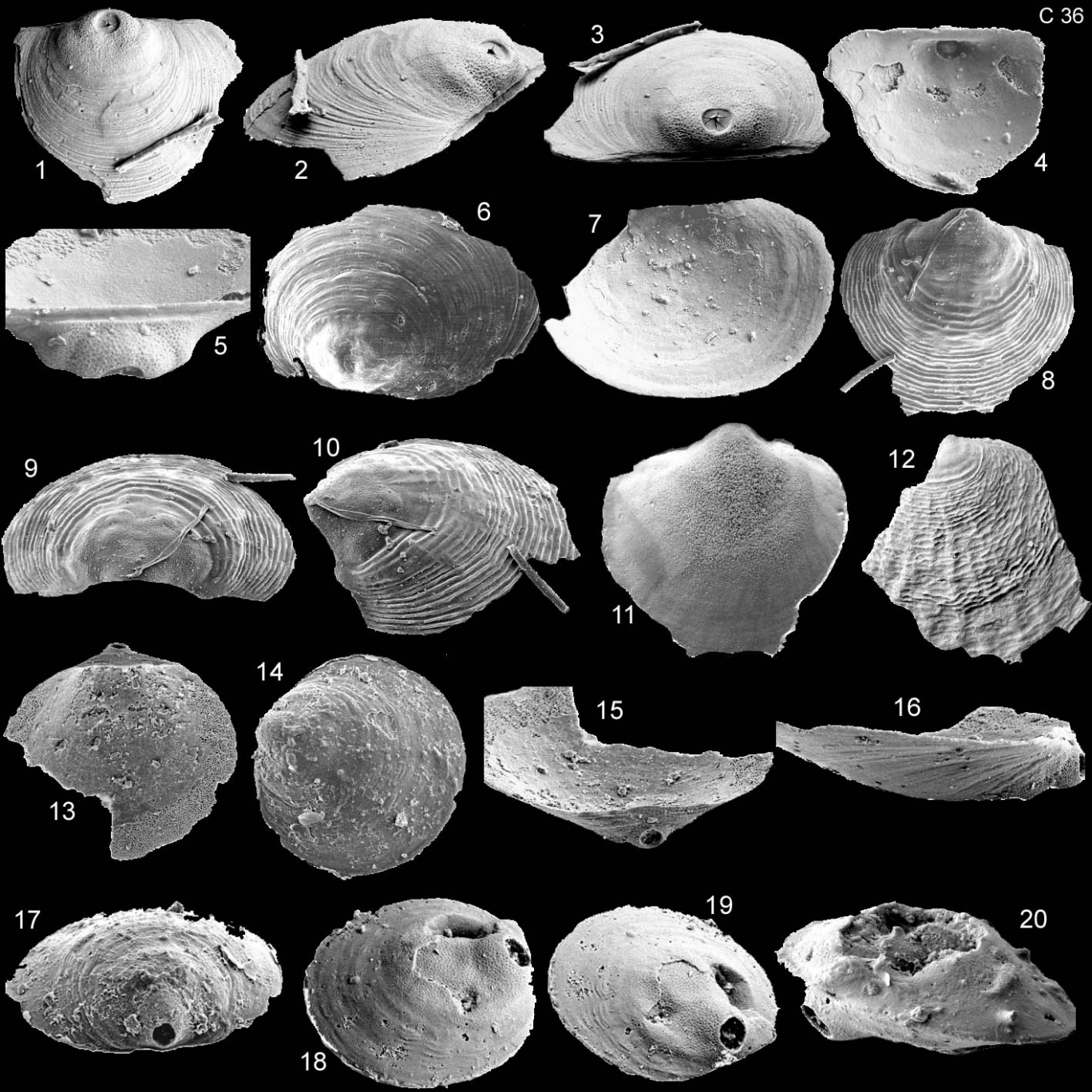
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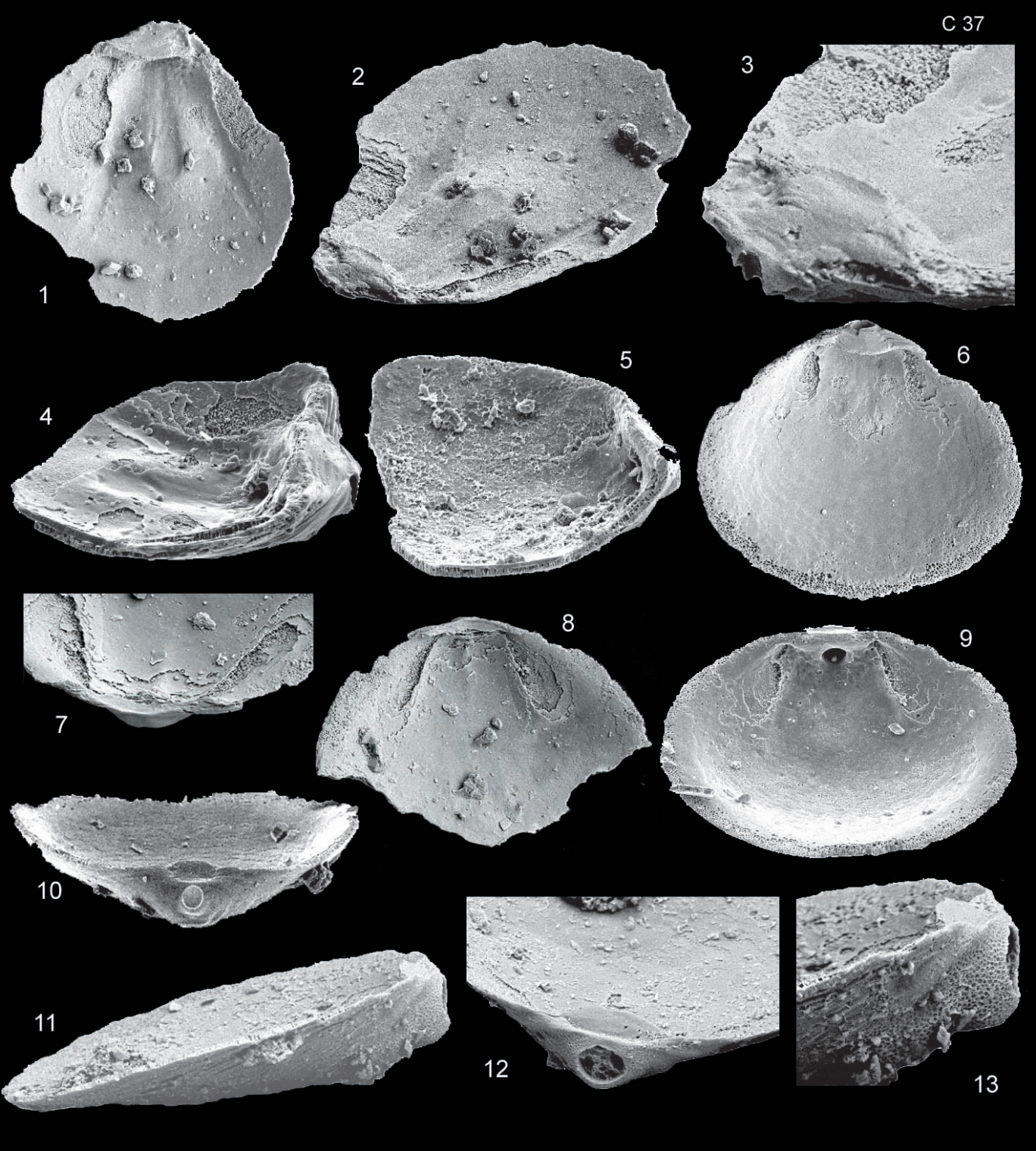
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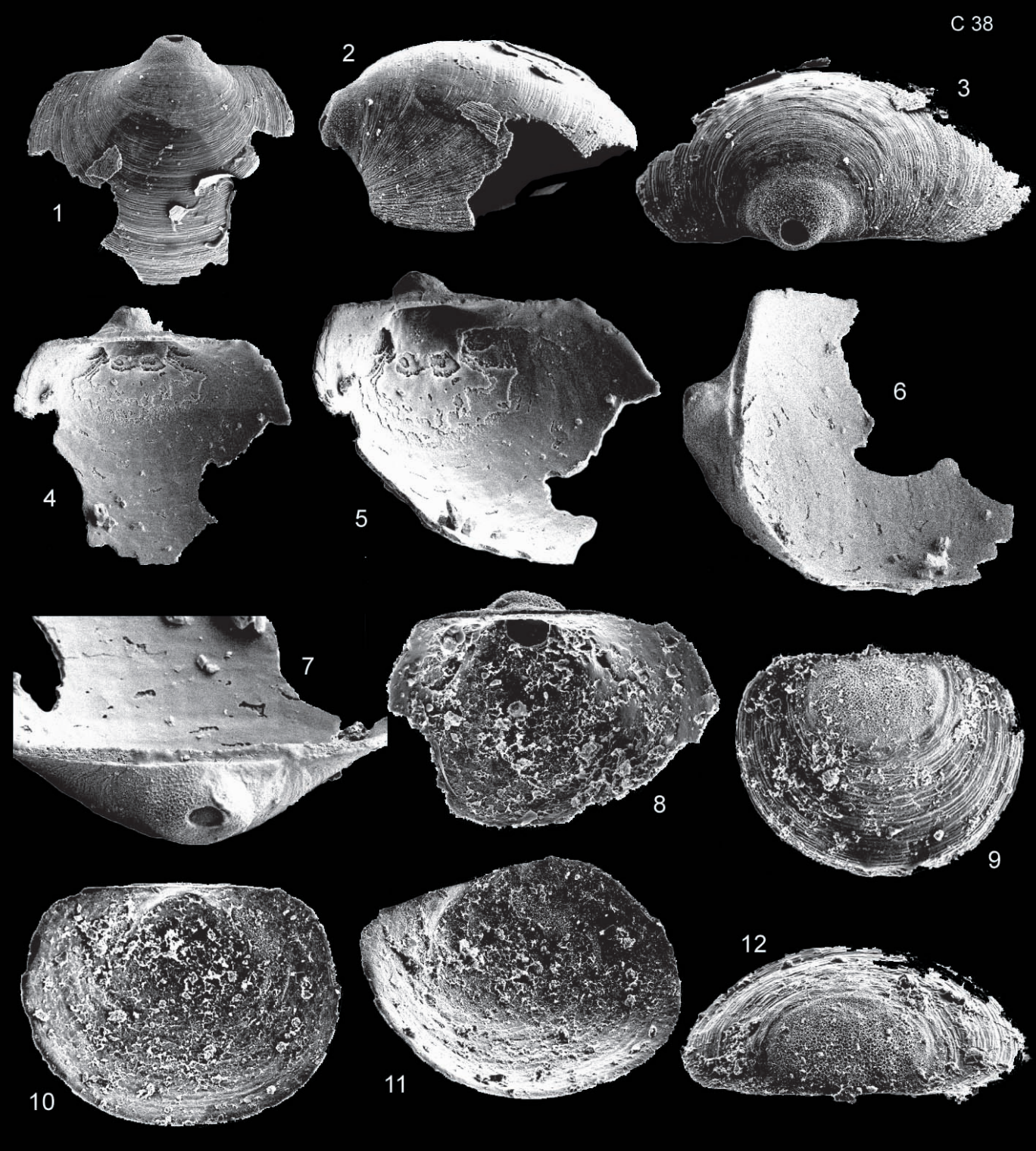
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EARLY LATE CAMBRIAN LINGULIFORMEAN BRACHIOPODS FROM THE DEADWOOD FORMATION OF SOUTH DAKOTA

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ABSTRACT

More than 2,200 fossil brachiopod valves of the subphylum Linguliformea, representing thirty-six species assigned to twenty-three genera, were recovered from two localities of the Deadwood Formation in the Black Hills of South Dakota. One new family, Holmerellidae, five new genera, *Amplitreta, Holmerellus*, *Dianabella*, *Ganotoglossa*, and *Vangaporosa* are erected and fifteen new species *Canthylotreta parislata, Quadrisonia? sigmoidea, Amplitreta cyclopis, Amplitreta elongata,* aff. *Anabolatreta tora, Opisthotreta nuda, Curticia pustulosa, Kotylotreta nupera, Holmerellus convexus, Holmerellus, acuminatus, Holmerellus limbatus, Dianabella artemesia, Ganotoglossa leptotropis, Tropidoglossa costata*, and *Vangaporosa dakotaensis* are described.

Based on a comparison of the brachiopod assemblages at the two localities with those from the Deadwood Formation of the Alberta subsurface, and with similar assemblages from Australia, the sections studied are determined to be late Marjuman (early Late Cambrian) in age, and correspond to the late Boomerangian to Mindyallan stages of Australia. Additionally, a map of hypothetical gyre patterns (large-scale ocean circulation cells) for the Late Cambrian is proposed to account for the relatively large number of linguliformean taxa that are shared in common between Laurentia, Kazakhstan and Australia.

INTRODUCTION

Phosphatic shelled brachiopods of the subphylum Linguliformea, formerly known as the class Inarticulata, though relatively rare today, were important

constituents of benthic ecosystems in the Lower Palaeozoic, particularly in the Cambrian. As such, understanding the linguliformean faunas and their role and interrelationships in ancient ecosystems opens a vital window into lower Palaeozoic palaeoecology and biostratigraphy. Although the Linguliformea are understudied compared to many other fossil groups, the work of a small number of specialists over the past thirty years has resulted in a wide-ranging revision of linguliformean systematics. Nonetheless, the Linguliformea remain poorly known, or undescribed altogether, from many regions of the world and a great deal of work needs still to be done.

Cambrian brachiopods from the Williston Basin area in Montana, including the Deadwood Formation, have been studied by Bell (1941, 1944), and Lochman (1964). Linguliformeans are nearly ubiquitous in the Black Hills of South Dakota, and distinctive, beautifully preserved shells of *Dicellomus* can be seen on the bedding surfaces of many sandstone units. Nonetheless, linguliformean brachiopods from the Black Hills have been studied only superficially, as summarized by Walcott (1912), and such studies were made prior to the application of acetic acid etching, as introduced by Bell (1948) to recover phosphatic fossils from insoluble residues and were often unable to distinguish the fine details of internal shell morpology necessary for accurate identification.

This monograph describes the linguliformean brachiopod faunas collected from shallow-water carbonate rocks at two localities in the northern Black Hills (Fig. 1), and is the second part of an ongoing study of the brachiopod fauna of the

Deadwood Formation that began with the description of the faunas from the subsurface of Alberta and Saskatchewan (Robson et al., 2003).

GEOLOGICAL SETTING

The Black Hills were formed by a basement uplift during the Eocene as part of the Laramide orogeny, and their core consists of Precambrian granite, and schistose and quartzose metamorphic rocks. In the Black Hills, the Deadwood Formation unconformably overlies the Precambrian basement and consists of an oval belt of outcrops dipping away from the centre of the uplift (Stitt, 1998).

The Deadwood Formation is a lithologically variable unit deposited in a shallow intracontinental sea far shoreward of the passive margin of western Laurentia during the Middle to Late Cambrian and Early Ordovician, and though it is geographically situated within the Williston Basin, deposition predates the origin of the basin. At the type section in Deadwood, South Dakota, as described by Darton (1901), the Deadwood Formation is approximately 125 m thick and consists of a thin interval of basal conglomerate and sandstone, followed by a thick succession of shale, limestone, and pebble-clast conglomerate, which is overlain by glauconitic sandstone and shale. The Deadwood Formation thickens northward, to a maximum of 270 m near the centre of the Williston Basin (Hein and Nowlan, 1998). In the Little Rocky Mountains of north-central Montana it is known as the Emerson Formation.

One of the most distinctive features of the Deadwood Formation is its intraclastic flat-pebble conglomerate, which can be composed of either limestone or

calcareous sandstone. These are interbedded with cross-laminated sandstone, siltsonte, and shale. This type of conglomerate, with clasts that are imbricated and often have rounded edges, is commonly thought to be the product of high-energy storm events, although Pratt (2002) has hypothesized that some may have been the result of tsunamis sweeping across the shallow epeiric sea. Many of the brachiopods described in this study were recovered from the matrix of carbonate flat-pebble conglomerates and are preserved unbroken, which would argue against such an extraordinarily violent event. Conversely, samples collected from identical lithologies of the Deadwood Formation in the Little Rocky Mountains of Montana, where Pratt conducted his study, contained large quantities of brachiopod shell fragments, but not a single intact valve was recovered. In any case events of varying energy levels that eroded the incipiently cemented sea floor also swept shells and bioclasts together, reworked them by wave action, but with minimal transport.

LITHOLOGY OF STUDY AREA

The sections studied represent the initial transgression of an epeiric sea over the Precambrian craton during the Sauk II sequence in the Marjuman Stage. The stratigraphic section at Pole Creek (locality B) demonstrates the transition from sandstone to carbonate rocks, probably representing a gradual deepening as transgression progressed (Fig. 2).

Unit B-1 is a 12 m thick sequence of thick- to massive-bedded nodular, coarse-grained, quartz arenite. This lithology is consistent with that of units

immediately overlying the basal conglomerate unit of the Deadwood Formation. No fossils were found.

Unit B-2 is a 2.5 m thick sequence of thin- to medium-bedded, medium-grained sandstone with interbeds of fine-grained glauconitic sandstone. Burrows are abundant, and numerous valves of the brachiopod *Dicellomus* were present on the surface of bedding planes, but cannot be extracted by acetic acid digestion.

Unit B-3 is a 4.7 m thick sequence of massive-bedded, fine-grained sandstone. Occasional valves of *Dicellomus* were present on bedding surfaces as in unit 2.

Unit B-4 is a 5 m thick sequence of thinly interbedded shale, limestone, and intraclastic flat-pebble conglomerate. The limestone and conglomerate contained an abundant and diverse fauna of brachiopods.

Unit B-5 is a 4 m thick sequence of thin interbeds of shale and sandstone with scattered lenses in the sandstone beds were composed of limestone and containing abundant brachiopods.

The 9 m thick section at locality A (Fig. 3) has a uniform lithology of flat-pebble clast conglomerate, which contained a sparse, low diversity fauna of brachiopods except at the top of the section (A-1-8), which had an extraordinarily abundant, but low-diversity fauna.

BIOSTRATIGRAPHY AND FAUNAL ASSEMBLAGES

Ten linguliformean species were recovered from the 9 m thick section at locality A, (Fig. 3), and twenty-nine species from the upper 9 m of the section at locality B (Fig. 4).

Stilpnotreta magna Henderson and MacKinnon, 1981 was recovered from the lowest interval (A-1-1) of locality A. This species is known from the upper Boomerangian to Mindyallan stages of western Queensland and New Zealand, which correspond to the *Cedaria* and *Crepicephalus* zones of the upper Marjuman Stage (early Late Cambrian) of North America. *Stilpnotreta magna* is also present in a 22 m thick interval of the Deadwood Formation in the Alberta subsurface (Robson et al., 2003). Although González-Gómez (2005) claimed that *Stilpnotreta* and *Neotreta* are exclusively Middle Cambrian taxa, *Stilpnotreta magna* Henderson and MacKinnon, 1981 and *Neotreta davidi* Popov, Berg-Madsen, and Holmer, 1994 are are found in the early Upper Cambrian of the Deadwood Formation, and *Neotreta humberensis* Robson and Pratt, 2001 is found in the early Late Cambrian of the Shallow Bay Formation in western Newfoundland, and have yet to be reported from the Middle Cambrian in Laurentia. *Apsotreta orifera* Palmer, 1954 was recovered from the uppermost interval (A-1-8) of locality A. *Apsotreta orifera* was originally described from the *Cedaria* and *Crepicephalus* zones in Texas. The section of the Deadwood Formation at locality A can therefore be confidently assigned an age of late Marjuman (early Late Cambrian).

Six species of *Dicellomus* were recovered from the lower carbonate intervals, and valves of *Dicellomus* sp. were found throughout most of the carbonate sequence (B-4-1 to B-5-1) of locality B. Numerous unidentified valves of *Dicellomus* were found in the sandstone intervals B-2 and B-3. *Dicellomus* is considered to be an index to the early Late Cambrian *Cedaria* and *Crepicephalus* zones (Bell, 1944) and, although no species of *Cedaria* are known from the Black

Hills, the *Cedaria* Zone is replaced locally by the equivalent *Cedarina dakotaensis* Zone (Stitt, 1998). Only two linguliformean species, *Eoscaphelasma* cf. *satpakensis* Koneva, Popov, and Ushatinskaya, 1990 and *Opisthotreta nuda* n. sp., were recovered from the upper interval of the section. *Eoscaphelasma* and *Opisthotreta* are both Late Cambrian genera, and *Opisthotreta nuda* also occurs (identified as *Opisthotreta* sp.) in a 9 m thick interval in the Alberta subsurface of early Late Cambrian (late Marjuman) age (Robson et al., 2003). With the exception of the unfossiliferous 12 m interval of quartz arenite at the base of the section (B-1), locality B is assigned an age of late Marjuman (early Late Cambrian).

Localities A and B are considered to be contemporaneous because they share several species in common and, according to the recent trilobite biostratigraphy of Stitt (1998) and Stitt and Perfetta (2000), correspond to the lowermost part of the Deadwood Formation in South Dakota.

As shown in Figure 5, the fauna from the flat-pebble limestone conglomerate at locality A is dominated by genera of the order Acrotretida, particularly at interval A-1-8, where *Canthylotreta parislata* n. sp. makes up over 60% of the nearly 900 valves recovered. This contrasts sharply with the faunal composition of unit B-4 (Fig. 6) at locality B, which is dominated by lingulids of the families Holmerellidae and Zhanitellidae. The faunal composition changes abruptly in unit B-5 (Fig. 7), where initially no one genus is dominant, but at the top of the unit (B-5-3) the acrotretid *Opisthotreta* accounts for the majority of the fauna. Thus throughout the succession there appears to be a shift in dominance from lingulids to acrotretids, and

since these units are all approximately contemporaneous, the faunal shift was probably due to local environmental change.

Dicellomus is widespread throughout the Deadwood Formation and is one of the most readily recognizable fossils, found in a wide variety of lithologies. As such, it appears to be largely unrestricted by facies and though it seemed to thrive best in shallow sandy substrates, it persisted throughout the transgression and occurs, in lesser abundance, in the somewhat deeper water limestone and flat-pebble conglomerate.

Of particular note is the distribution of the three species of *Holmerellus* n. gen., which dominated the fauna in the lowermost intervals of unit B-4. *Holmerellus* accounted for 60% of more than 500 valves recovered from interval B-4-1, diminished slightly to 50% of nearly 150 valves from the overlying interval, B-4-2, but is completely absent in overlying horizons. This change reflects, at least, a localized extinction that does not appear to be attributable to, or reflected by, any change in the depositional environment.

In unit B-5, the lithology changes from interbedded of shale, limestone, and flat-pebble conglomerate, to interbeds of shale and sandstone. Fossils from this horizon were recovered from limestone lenses in the sandstone and may have acumulated in ripple troughs. Twelve species were recovered from the lowest horizon of the interval (B-5-1), and only one of these, *Lingulepis* cf. *acuminata*, was found at the interval 2 m above (B-5-3). The other two species recovered from the top of the section, *Opisthotreta nuda* and *Eoscaphelasma* cf. *satpakensis*, are present in the uppermost horizon of the underlying interval (B-4-5), but absent at B-

5-1 then reappeared at B-5-3. This suggests that the changing depositional environment was unfavourable to most of the fauna in the area. Only *Lingulepis* cf. *acuminata* was present at every fossiliferous interval of the section, suggesting that it was tolerant of a variety of environments.

BIOGEOGRAPHY AND DISTRIBUTION

Many species of linguliformean brachiopods have a nearly cosmopolitan distribution and there seems to be a particularly strong connection between Upper Cambrian species of acrotretids from Australia, Kazakhstan, and Laurentia (e.g. Rowell and Henderson, 1978; Robson and Pratt, 2001; Robson et al., 2003). This is reflected especially by the Deadwood Formation, which yields some acrotretid taxa, such as *Apsotreta* in the Black Hills and *Linnarssonella* in the subsurface of Saskatchewan, that are endemic to Laurentia, but also many taxa of cosmopolitan acrotretids that are also found in Kazakhstan, and Australia. *Dactylotreta redunca*, *Kotylotreta undata*, and *Stilpnotreta magna* described in this study, are also known from Kazakhstan and Australia. Furthermore several new species and species left in open nomenclature are assigned to genera such as *Eoscaphelasma*, *Canthylotreta*, and *Physotreta* that are also found in Kazakhstan.

The widespread distribution of acrotretids could have been facilitated if they had planktotrophic larvae, which are free-swimming larvae characterized by the ability to feed upon planktic food, thereby reducing the amount of yolk necessary in the egg and allowing for a longer larval duration (Jablonski and Lutz, 1983). Scheltema (1967) divided planktotrophic larvae into two developmental stages: the

precompetent stage, in which the larva undergoes growth and development, and the competent stage, in which the development is essentially complete, but the planktic lifestyle is retained until the larva finds a suitable settlement site. There are several advantages to planktotrophic development: (1) it provides a means of widespread dispersal due to a prolonged larval stage; (2) larvae that are able to feed independently do not require a large metabolic investment from the parent in terms of yolk production; and (3) selection of a preferred substrate is possible. These advantages are offset, however, by a high mortality rate due to predation of the larvae within the plankton. In addition, whereas each individual larva is metabolically inexpensive to the parent, a great number must be produced in order to insure that sufficient numbers survive to settlement.

Jablonski and Lutz (1983) suggested that acrotretids, because of their small size, may not have been able to produce a sufficient quantity of offspring to offset predation, and therefore may not have had plankotrophic larvae. Nonetheless, it is becoming increasing apparent that many acrotretid species do have a widespread distribution and likely did have a planktotrophic existence for at least part of their larval stage.

The habit of planktotrophy in marine invertebrate larvae tends be inversely proportional to latitude: the greatest number of planktotrophic species occur at low latitudes and decrease towards the poles, whereas species living at higher latitudes predominantly include non-planktrophic, direct-developing larvae (Valentine and Jablonski, 1983). In the Late Cambrian, Laurentia, Kazakhstan, and Australia were

located at low latitudes, and so brachiopods native to these areas could, indeed, have been planktotrophic.

Unlike living rhynchonelliformeans, which are nonplanktotrophic and do not begin to develop a shell until after settlement (Chuang, 1977), linguliformeans have shelled larvae, which was pitted in many taxa, including all acrotretids. Biernat and Williams (1970) interpreted pits in the larval shells to be the moulds of a vesicular periostracum, while von Bitter and Ludvigsen (1979) considered them to be the result of resorption intended to reduce the weight of the larval shell to increase buoyancy, citing overlapping and cross-cutting of pits was as evidence for resorption. Since the discovery by Williams et al (1998) and Cusack et al (1999) that the pits of larval shells of living discinid brachiopods are the impressions of siliceous tablets, Williams (2003) suggested that many of the larger, flat-bottomed or spherical pits, found in many fossil specimens may also be impressions of mineralized tablets. The functional and ecological significance of larval pits is not well understood, and comparison of pit morphology to species distribution has never been made.

The effect of dispersal on biogeography

There are two principle means by which benthic species are distributed widely and rapidly: (1) passive transport, in which planktic larvae float in ocean currents, and (2) rafting, whereby larvae or adults attach to objects adrift in the sea (Scheltema, 1977). Thorson (1961) studied 195 species of benthic invertebrates and concluded that their period of larval development was usually too short to account for larval transport across major zoogeographic barriers. He found that the pelagic

stage lasts an average of two to six weeks and, in this time, if carried by a current with a velocity of 0.5 km/hr they can drift 150-500 km. However, some benthic invertebrates have larvae whose pelagic stage can last between six months and one year, which Scheltema (1971) termed "teleplanic larvae," and these could potentially drift 2,100-4,400 km.

Zinsmeister and Emerson (1979) suggested that oceanic currents provide one-way corridors of passive larval dispersal, and therefore distribution of fossil faunas can be useful in reconstructing ancient current patterns, or for testing hypotheses concerning palaeocurrents derived from other geological and geophysical data. Although, as Scheltema (1977) points out, surface circulation patterns are complex and larvae will seldom be carried over a direct route between two points, a general notion of the current direction and speed can be determined.

All main oceanic currents are components of large-scale global circulation patterns called gyres, which are produced by the Coriolis Effect and are characterized by patterns of equatorial symmetry. The size, shape, and distribution of gyres are dictated by the position of continental landmasses, and it may be possible to infer the disposition of gyres at various times in the past by modifying present day gyre cells to fit the geographic confines of ancient oceans, while retaining the cells' general pattern of equatorial symmetry.

MATERIALS AND METHODS

Brachiopods were recovered from samples of limestone and flat-pebble conglomerate collected from two localities of the Deadwood Formation in the Black

Hills of South Dakota (Fig. 1). Locality A is a roadcut approximately 5 km south of Deadwood, and locality B is an outcrop at Pole Creek, approximately 15 km southwest of Deadwood. The rock samples were dissolved in a 10 percent solution of acetic acid and phosphatic brachiopod valves were picked from the insoluble residue using a fine sable brush. These were carefully washed and sieved, then sorted into taxa, mounted on aluminum stubs, gold coated, and examined and digitally photographed using scanning electron microscopy. Figured specimens are housed in the collections the United States National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C.

SYSTEMATIC PALEONTOLOGY

Class LINGULATA Gorjansky and Popov, 1985

Order ACROTRETIDA Kuhn, 1949

Family ACROTRETIDAE Schuchert, 1893

Subfamily ACROTRETINAE Schuchert, 1893

Genus APSOTRETA Palmer, 1954

Type species.--*Apsotreta expansa* Palmer, 1954.

Other species.--*Apsotreta orifera* Palmer, 1954; *Apsotreta attenuata* Kurtz, 1971; *Apsotreta stricta* Kurtz, 1971.

Diagnosis.--Shell subcircular with short, convex posterior margin. Ventral pseudointerarea apsacline to catacline with interridge; propareas not defined. Foramen small, posteriorly directed, contained within larval shell. Internal foramen

penetrates broad, ridge-like apical process. Apical process occludes apex, extending predominantly along anterior slope with long parallel or anteriorly expanding margins. Dorsal pseudointerarea with broad, triangular median depression and short orthocline to anacline propareas; buttressed by low posterior median ridge. Median septum triangular to blade-like.

Occurrence.--Upper Cambrian of Texas, Missouri, and South Dakota.

Discussion.--*Apsotreta* is distinguished by its long ridge-like apical process, perforated by the internal foramen. *Canthylotreta* Rowell, 1966 has a similar apical process that is not perforated by the internal foramen but, rather, is located just ventral of the foramen. The dorsal valves of the two genera are very similar and difficult to distinguish. Zell and Rowell (1988) noted that the dorsal valves could be distinguished by the lack of a dorsal sulcus in *Apsotreta*. Although Palmer (1954) described the dorsal valves of *Apsotreta* as having a shallow sulcus, none of the dorsal valves of *Apsotreta orifera* described here are sulcate.

APSOTRETA ORIFERA Palmer, 1954

Plate 1, figures 1-9

Apsotreta orifera PALMER, 1954, p. 771, pl. 90, figs. 15, 16, 18.

Diagnosis.--Ventral valve slightly apsacline to catacline. Apical process high, strongly developed, nearly parallel-sided; penetrated by relatively large internal foramen. Apical pits located in beak adjacent to internal foramen. Median septum high, blade-like, extending from hourglass-shaped posteromedian ridge.

Description.--Shell subcircular with ornament of fine growth lines. Posterior margin short, convex.

Ventral valve subconical. Pseudointerarea catacline, with median ridge; propareas not defined. External foramen contained within larval shell, posteriorly directed. Internal foramen penetrates high, long, robustly developed apical process. Apical process occludes apex, extending from apical region of posterior slope to one-half length of anterior slope. Deep groove extends anteriorly from internal foramen bounded by high margins, normally parallel-sided, but expanding anteriorly in some specimens. Dorsal surface of apical process normally broken anterior to foramen. Apical pits located in beak adjacent to internal foramen. *Vascula lateralia* baculate, diverging anteriorly from apical pits. Cardinal muscle scars located on posterolateral valve slopes.

Dorsal valve gently convex. Pseudointerarea short, with triangular median depression and narrow, orthocline propareas. Broad hourglass-shaped median ridge buttresses median depression, extending nearly one-half of valve length. Median septum narrow, blade-like, extending from anterior region of median ridge to near anterior valve margin. Cardinal muscle scars elongate, located near posterolateral valve margins.

Material examined.--Thirteen ventral valves and thirteen dorsal valves from locality A, Black Hills, South Dakota.

Occurrence.--Lower Upper Cambrian (Marjuman stage) of Texas and South Dakota.

Discussion.--The specimens described here differ from the type material only in having a catacline ventral pseudointerarea. The specimens of *Apsotreta orifera* described by Palmer (1954) are only very slightly apsacline, not considered here to be a significant difference.

APSOTRETA sp.

Plate 1, figures 10-13

Description.--Ventral valve steeply conical. Pseudointerarea catacline to slightly apsacline with well-defined, narrow intertrough. Pedicle foramen small, circular, posteriorly directed, contained within larval shell. Apical process low, nearly parallel sided, penetrated posteriorly by minute pedicle tube. Apical pits minute, located directly lateral to internal foramen on either side of apical process. Cardinal muscle scars located on posterolateral slopes. *Vascula lateralia* baculate, diverging anteriorly from apical pits.

Material examined.--Four ventral valves from locality B, Black Hills, South Dakota.

Occurrence.--Lower Upper Cambrian (Marjuman stage) of South Dakota.

Discussion.--*Apsotreta* sp. is similar to the type species in having a minute internal foramen but, unlike *A. expansa*, its apical process does not diverge anteriorly, nor is its pseudointerarea strongly convex. *Apsotreta* sp. has an apical process similar to that of *A. orifera*, but it is not as high, nor as well developed. It also differs from *A. orifera* in having a minute rather than a relatively large internal foramen.

Genus CANTHYLOTRETA Rowell, 1966

Type species.--*Acrotreta marjumensis* Walcott, 1908.

Other species.--*Canthylotreta grada* Zell and Rowell,1988; *Canthylotreta atasuica* Holmer, Popov, Koneva and Bassett, 2001; *Canthylotreta* sp. Holmer, Popov, Koneva and Bassett, 2001; *Canthylotreta parislata* n. sp.

Diagnosis.--Shell outline transversely oval to subtriangular; ventribiconvex; ornament of fine growth lines. Ventral valve apsacline to procline. External foramen small, circular, posteriorly directed. Apical process subtriangular, located ventrally to, and extending anteriorly from, internal foramen; nearly parallel-sided posteriorly, expanding anteriorly in some species. *Vascula lateralia* diverge anteriorly from small apical pits located adjacent to internal foramen. Dorsal valve gently convex, sulcate. Pseudointerarea with depressed median plate and anacline to orthocline propareas. Median septum high, triangular, continuing posteriorly as low ridge, expanding to buttress median plate.

Occurrence.--Middle to Upper Cambrian of Utah, Nevada and South Dakota; North Greenland; Kyrgyzstan; and Kazakhstan.

Discussion.--As noted by Rowell (1966) and Zell and Rowell (1988), *Canthylotreta* most closely resembles *Apsotreta* Palmer, 1954. The apical processes of the two genera are similar, distinguished primarily in that the internal foramen penetrates the apical process of *Apsotreta*, but is located dorsally to the apical process in *Canthylotreta*. Another noticeable difference is that the dorsal valves of *Canthylotreta* have a shallow sulcus, a feature lacking in *Apsotreta*.

CANTHYLOTRETA PARISLATA new species

Plate 2, figures 1-17

Diagnosis.--Shell transversely oval in outline. Ventral valve catacline; apical process with parallel margins; external foramen not contained within larval shell. Dorsal pseudointerarea with short, straight, orthocline propareas. Median septum low, short, blade-like, extending one third of valve length, occupying central third of valve.

Description.--Shell transversely oval in outline, ornamented with fine, concentric growth lines. Fine, radial costae present in juvenile region of shell, disappearing towards margins.

Ventral valve catacline; pseudointerarea poorly developed with broadly triangular intertrough. Posterior margin short, straight. Beak overhangs posterior margin; external foramen small, circular, posterodorsally directed, not contained within larval shell. Internal foramen penetrates posterior valve wall just dorsal to apical process. Apical process low to moderate, extending from internal foramen anteriorly to one-third valve length, rising slightly to form low peak at anterior extent. Anterior peak broken in most specimens. Lateral margins of apical process parallel, bounding shallow dorsal groove that extends directly from internal foramen to anterior peak. Apical pits located lateral to internal foramen. *Vascula lateralia* baculate, diverging anteriorly from apical pits to one-half valve length. Cardinal muscle scars elongate, located on posterolateral valve slopes.

Dorsal valve moderately convex, sulcate. Pseudointerarea with short orthocline propareas separated by depressed median plate. Broad, low median ridge buttressing median plate extends anteriorly from pseudointerarea to three-eighths of valve length. Low, narrow, blade-like median septum extends posteriorly from anterior extent of median ridge to approximately two-thirds of valve length, rising only slightly beyond the plane of the commissure. Cardinal muscle scars posteriorly located, just anterior to pseudointerarea on either side of median ridge.

Etymology.--Latin, *paris*, equal; *latus*, side. Named for parallel-sided apical process.

Types.--Holotype, USNM 527103, ventral valve: Deadwood Formation, Black Hills, South Dakota.

Other material examined.--Two hundred and ninety ventral valves and ninety dorsal valves from locality A, Black Hills, South Dakota.

Occurrence.--Lower Upper Cambrian (Marjuman stage) of South Dakota.

Discussion.--*Canthylotreta parislata* n. sp. is most similar to the type species, and the most significant differences between them are that *C. parislata* has a catacline rather than apsacline ventral valve, the external foramen is not contained within the larval shell, and the dorsal propareas are orthocline rather than anacline. The apical process of *Canthylotreta parislata* tends to parallel-sided whereas the apical process of *C. marjumenis* tends to expand anteriorly with a subtriangular outline. This is a variable feature however, and in some specimens of *Canthylotreta parislata* the slopes of the anterior peak of the apical process extend laterally as well as anteriorly creating an appearance of anterior expansion. In other specimens the

anterior peak of the apical process was tapers anteriorly. In the majority of specimens examined here, however, the anterior edge of the apical process terminates in a U-shaped slope maintaining parallel margins throughout the entire length of the apical process.

CANTHYLOTRETA sp.

Plate 3, figures 1-6

Description.--Ventral valve slightly apsacline with shallow intertrough. Beak overhangs straight posterior margin; external foramen elongate oval, directed posterdorsally, not contained within larval shell. Internal foramen large, circular, penetrating posterior wall of valve. Apical process ventral to internal foramen, expanding anteriorly with shallow groove on dorsal surface leading to foramen. Cardinal muscle scars located on posterolateral slopes. Apical pits not apparent. *Vascula lateralia* weakly impressed

Material examined.--One ventral valve from locality 'B,' Black Hills, South Dakota.

Occurrence.--Lower Upper Cambrian (Marjuman Stage) of South Dakota.

Discussion.--*Canthylotreta* sp. is known only from a single fragmented ventral valve. Though the apical process and internal foramen is similar to that of *Canthylotreta marjumensis* Rowell,1966, its elongate oval external foramen is strikingly different. All previously described species of *Canthylotreta* have a small, circular external foramen.

Genus DACTYLOTRETA Rowell and Henderson, 1978

Type species.--*Dactylotreta redunca* Rowell and Henderson, 1978.

Other species.--*Dactylotreta solitaria* Popov (in Solovjev et al., 1984); *Dactylotreta patriella* Zell and Rowell, 1988; *Dacytylotreta* sp. Henderson (in Henderson et al., 1992); *Dactylotreta batkanensis* Popov and Holmer, 1994; *Dactylotreta pharus* Popov and Holmer, 1994; *Dactylotreta sanjuanensis* Holmer, Popov, and Lehnert, 1999; *Dactyolotreta septata* Holmer, Popov, Koneva, and Basset, 2001; *Dactylotreta prisca* Mergl, 2002.

Diagnosis.--See Holmer and Popov (2000).

Occurrence.--Middle Cambrian to Lower Ordovician of Antarctica, Argentina, Austrialia (Queensland), Bohemia, Canada (western Newfoundland), North Greenland, Kazakhstan, Norway, Russia (South Urals), Sweden, and the U.S.A (Great Basin and South Dakota).

DACTYLOTRETA REDUNCA Rowell and Henderson, 1978

Plate 4, figures 1-9

Dactylotreta redunca ROWELL AND HENDERSON, 1978, p. 4, text figs. 2, 3, pl.1, figs. 1-8.

Diagnosis.--Ventral valve catacline; beak incurved, extending beyond posterior margin. Pseudointerarea poorly defined with shallow, narrow intertrough. Dorsal valve elongate subcircular, nearly flat in profile; psuedointerarea anacline. Posterolateral margins nearly straight, forming pointed apex with angle of

approximately 120˚. Median septum expands posteriorly to form buttress continuous with pseudointerarea. Margins with flattened limbus.

Description.--Ventral valve highly conical. Catacline in profile with incurved beak extending beyond posterior margin; posterior slope slightly concave. Posteriorly directed foramen contained entirely within larval shell, continues internally as short pedicle tube. Pseudointerarea poorly defined with shallow, narrow intertrough. Apical process large, entirely occluding apical one-third of valve. Apical pits located on either side of internal foramen. Cardinal muscle scars large, oval, located lateral to apical pits on posterolateral slope of valve walls. Mantle canals not apparent.

Dorsal valve longer than wide, elongate subcircular in outline; shallowly convex, nearly flat in profile. Posterolateral margins nearly straight, forming pointed apex with angle of approximately 120˚. Lateral and anterior margins with flattened limbus. Pseudointerarea anacline with well defined, narrow, triangular propareas separated by broad, concave median plate. Narrow blade-like median septum rises anteriorly to maximum height near anterior margin; septum expands posteriorly to form buttress continuous with median plate of pseudointerarea. Cardinal muscle scars large, oval, located on either side of buttress on posterolateral slope of valve walls.

Material examined.--Ten ventral valves and one dorsal valve from locality B, Black Hills, South Dakota.

Occurrence.--Upper Cambrian (uppermost Idamean Stage to lowermost Iverian Stage) of western Queensland; lower Upper Cambrian (uppermost Marjuman stage) of South Dakota.

Discussion.--This is the first reported occurrence of *Dactylotreta redunca* in North America, further illustrating the faunal link, demonstrated by Rowell and Henderson (1978) and Robson et al. (2003), between Australia and Laurentia among linguliformean brachiopods. The specimens described here accord in all respects with the type material as described by Rowell and Henderson (1978), and no regional intraspecific variation in morphology has been observed. *Dactylotreta redunca* occurs stratigraphically lower in Laurentia than in Australia, as the *Cedaria* and *Crepicephalus* zones correspond roughly to the *Erediaspis eretis* to *Glyptognostus stolidotus* zones (upper Boomerangian to Mindyallan stages) in Australia.

Genus PHYSOTRETA Rowell, 1966

Type species.--*Acrotreta spinosa* Walcott, 1905.

Other species.--*Physotreta rugosa* Popov (in Nazarov and Popov, 1980); *Physotreta deformis* Holmer, 1989.

Diagnosis.--Shell subcircular with concave to convex posterior margin. Ventral valve moderately conical. Pseudointerarea poorly defined, procline to catacline with shallow intertrough. Foramen contained completely within larval shell. Apical process occluding apex, perforated by pedicle tube. Apical pits

located lateral to foramen. Dorsal pseudointerarea anacline with broadly triangular median depression and median buttress.

Occurrence.--Upper Cambrian of the United States (Nevada and South Dakota), Ordovician of Sweden and Kazakhstan.

Discussion.--The diagnosis has been modified only slightly from that of Holmer and Popov (2000) to reflect the expanded range of morphological features found in *Physotreta spinosa* as described below. These include a slightly concave rather than exclusively flat or convex posterior margin, a foramen contained by the larval shell, but not necessarily tangential to the shell margin, and an ornament that ranges from fine growth lines to rugae.

PHYSOTRETA SPINOSA Walcott, 1905

Plate 4, figures 10-17

Acrotreta spinosa WALCOTT, 1905, p. 302; WALCOTT, 1912, p. 713, pl. 79, figs 4, 4', 4", 4a-g.

Physotreta spinosa (Walcott, 1905), ROWELL, 1966, text figs. 20-23, pl. 3, figs. 15-35.

Diagnosis.--Shell ornamented with discontinuous, irregular growth lamellae, or fine concentric growth lines. Ventral valve conical; catacline to procline. Apical process with shallow longitudinal groove on posterior slope; hollow U-shaped pit on anterior slope. Dorsal valve with deep median depression separated by narrowly triangular, anacline propareas. Median septum subtriangular blade with concave posterior and anterior slopes.

Description.--Ventral valve conical, subcircular in outline, catacline to procline. Beak incurved, extending slightly beyond posterior margin. Pseudointerarea poorly defined, flat in lateral profile, with shallow, narrow intertrough. Posterior margin slightly concave. Larval shell well defined, bulbous. Postlarval shell ornamented with fine concentric growth lines. Foramen contained entirely within larval shell, posteriorly directed, continuing internally as pedicle tube, perforating apical process, directed dorsally. Apical process extends from posterior slope to anterior slope, occluding apex. Posteriorly, apical process forms parallel-sided ridge with shallow longitudinal groove extending from internal foramen to posterior extent of ridge. Anteriorly, the sides of the apical process converge, merging with anterior slope of valve, U-shaped at anterior end. Dorsal surface of process on anterior slope hollow, forming large U-shaped pit just anterior to foramen. Apical pits located lateral to foramen. Cardinal muscle scars large, oval, located on posterolateral valve walls. *Vascula lateralia* deeply incised, extending from apical pits, diverging anteriorly.

Dorsal valve subcircular in outline. Pseudointerarea with wide, deeply depressed, delta-shaped median plate separated from acutely triangular anacline propareas by sharp flexure; medially buttressed by posterior thickening. Median septum high, with concave posterior and anterior slopes; anterior slope forming thickened ridge. Posterolateral muscle scars large, elongate, diverging anterolaterally.

Material examined.--Twelve ventral valves and nine dorsal valves from locality B, Black Hills, South Dakota.

Occurrence.--Upper Cambrian (Marjuman stage) of South Dakota and Upper Cambrian (Steptoean stage) of Nevada.

Discussion.--The specimens described here differ only in external features from those described by Rowell (1966) in being somewhat more conical, having a bulbous larval shell, and an ornamentation of fine concentric growth lines rather than discontinuous, irregular growth lamella. While Walcott (1905) named the species for spine-like nodes of thickened growth lamellae, Rowell (1966) noted that this is actually an uncommon feature of the species, present only two of sixteen ventral valves and no dorsal valves that he examined. This feature is not present in any of the specimens described here. The shallow groove on the dorsal surface of the apical process along the posterior valve slope extends from the dorsally directed foramen and, presumably, indicates where the pedicle rested.

Genus QUADRISONIA Rowell and Henderson, 1978

Type species.--*Quadrisonia minor* Rowell and Henderson, 1978.

Other species.--*Quadrisonia declivis* Koneva and Popov, 1988; *Quadrisonia suspensa* Koneva and Popov, 1988; *Quadrisonia simplex* Koneva, Popov, and Ushatinskya, 1990; *Quadrisonia* n. sp. (Henderson, in Henderson et al., 1992); *Quadrisonia*? sp. (Puura and Holmer, 1993); *Quadrisonia* cf. *minor* (Holmer, Popov, and Lehnert, 1999); *Quadrisonia*? sp. (Holmer, Popov, Koneva, and Bassett, 2001); *Quadrisonia*? *lavadamensis*, Popov, Holmer and Miller, 2002.

Diagnosis.--See Holmer and Popov (2000).

Occurrence.--Upper Cambrian of ?Utah, South Dakota, Argentina, Queensland, West Antarctica, ?Kazakhstan, ?Sweden.

QUADRISONIA? SIGMOIDEA new species

Plate 5, figures 1-13

Diagnosis.--Ventral pseudointerarea catacline with shallow intertrough. Apical process subtriangular with low base on anterior slope, tapering to slender ridge on posterior slope, perforated posteriorly by pedicle tube. Dorsal pseudointerearea anacline. Median septum high with sigmoid posterior slope, anterior slope concave.

Description.--Transversely oval in outline. Ventral valve moderately convex with flat to slightly convex posterior margin. Pseudointerarea broadly triangular, catacline with shallow, narrow intertrough. Pedicle foramen posteriorly directed, contained entirely within larval shell, continuing internally as short pedicle tube. Apical process subtriangular with broad, low base on anterior slope of valve, narrowing to slender ridge on posterior slope, perforated posteriorly by pedicle tube. Apical pits located on either side of foramen, adjacent to apical process. Mantle canals shallow, short extending from apical pits along anterolateral margins of apical process to less than one-half of valve length. Cardinal muscle scars small, circular, located on posterolateral valve walls.

Dorsal valve shallowly convex, sulcate. Pseudointerarea with broad, triangular median depression, buttressed by posterior expansion of median septum.

Propareas triangular, anacline. Cardinal muscle scars large, elongate. Median septum narrow with sigmoid posterior slope, concave anterior slope.

Etymology.--Named for elongate S-shaped (sigmoidal) posterior profile of dorsal septum.

Types.--Holotype, USNM 527118, ventral valve: Deadwood Formation, Black Hills, South Dakota.

Other material examined.--Four ventral and five dorsal valves from locality B, Black Hills, South Dakota.

Occurrence.--Lower Upper Cambrian (Marjuman Stage) of South Dakota.

Discussion.--*Quadrisonia*? *sigmoidea* differs from all other species of the genus in having an anacline dorsal pseudointerarea and high median septum. Most species of *Quadrisonia* have orthocline dorsal pseudointerareas and low median ridges, although the median septum is highly variable and is absent in some species (Rowell and Henderson, 1978), while rising above the level of the commissural plane in others (e.g. *Quadrisonia* sp. cf. Henderson, 1992). *Quadrisonia*? *sigmoidea* is most readily distinguished from other species by the sigmoidal profile of the dorsal median septum, the apsacline dorsal pseudointerarea, and the low subtriangular apical process that tapers to a slender ridge on the posterior slope of the ventral valve. It is because these features deviate significantly from the norm that *Quadrisonia*? *sigmoidea* is assigned only provisionally to the genus.

QUADRISONIA sp.

Plate 3, figures 7-13

Description.--Ventral valve procline with well-defined intertrough. Posterior slope convex, anterior slope nearly straight. External ornament of fine growth lines. Posterior margin slightly concave. External foramen oval, ventrally directed, not contained within larval shell. Apical process subtriangular with broad base on anterior slope of valve, narrowing posteriorly and extending to posterior slope of valve, perforated by posterodorsally directed internal foramen. Apical pits not apparent. Mantle canals not apparent. Cardinal muscle scars elongate, located on posterolateral valve slopes.

Material examined.--Four ventral valves from locality 'B,' Black Hills, South Dakota.

Occurrence.--Lower Upper Cambrian (Marjuman Stage) of South Dakota.

Discussion.--*Quadrisonia* sp. is known only from its ventral valves. It is distinguished by its convex posterior slope, and by the apparent absence of apical pits and mantle canals. *Quadrisonia* sp. undoubtedly represents a new species, but is not named due to insufficient material.

Subfamily LINNARSSONIINAE Rowell, 1965

Genus AMPLITRETA new genus

Type species.--*Amplitreta cyclopis* n. sp.

Other species.--*Amplitreta elongata* n. sp.

Diagnosis.--Shell ventribiconvex. Ventral valve catacline; maximum height occurring at approximately one-third of valve length from posterior margin. Posterior margin short, concave; beak overhangs posterior margin. Foramen large,

not contained within larval shell. Apical process low, subtriangular callosity located anterior of foramen. Dorsal valve gently convex with short, straight posterior margin. Pseudointerarea orthocline, undivided, with vestigial propareas. Low median ridge extends anteriorly from pseudointerarea to approximately three-quarters of valve length.

Etymology.--Latin, *amplus*, large; *tretos*, perforated.

Discussion.--*Amplitreta* n. gen. is distinguished by its catacline ventral valve with low subtriangular apical process, and large foramen. The foramen is enlarged by resorption, in some cases extending beyond the posterior margin.

Amplitreta is more similar to Lower and Middle Cambrian linnarssoniinaeans than to other Upper Cambrian genera of the subfamily. It is similar to *Opisthotreta* Palmer (1954) in having a poorly developed apical process and a short dorsal pseudointerarea with vestigial propareas, but the ventral valve of *Opisthotreta* differs significantly in having a strongly apsacline pseudointerarea and an elongate beak with the foramen contained within the larval shell.

Amplitreta shares many features in common with the Lower to Middle Cambrian genera *Aphelotreta* Rowell, 1980 and *Hadrotreta* Rowell, 1966. It is more similar to *Aphelotreta* in possessing a similar apical process, described by Rowell (1980) as a low subtriangular swelling that is indistinct in smaller specimens. *Amplitreta* differs from *Aphelotreta* mainly in the nature of its dorsal valve, which is much less convex, has a longer median ridge, and a straight posterior margin.

AMPLITRETA CYCLOPIS new species

Plate 6, figures 1-18

Pegmatreta sp. ROBSON AND PRATT, 2001, p. 247, figs. 6.1-6.8.

Diagnosis.--Larval shell relatively large; postlarval shell ornamented with high rugose ridges. Formamen large, circular, posteriorly directed, penetrating posterior valve wall with flange-shaped tube. Dorsal valve gently convex, posterior margin short, straight. Pseudointerarea orthocline with slight median depression.

Description.--Shell transversely oval. Larval shell relatively large, well defined. Postlarval shell ornamented with high, concentric rugose ridges.

Ventral valve moderately convex with maximum height near anterior margin of larval shell. Posterior margin concave. Pseudointerarea catacline with moderately developed intertrough. Larval shell occupying nearly half of shell exterior. Beak overhangs posterior margin; foramen large, circular, directed posteriorly and somewhat dorsally, not contained within larval shell. Internally, foramen penetrates posterior valve wall as small, flange-shaped tube produced by shell resorption. Apical process just forward of foramen, forming very low callosity with shallow groove leading to foramen. Cardinal muscle scars small, located on posterolateral slopes. Mantle canals very weakly impressed, baculate, diverging anteriorly from either side of apical process. Apical pits not apparent.

Dorsal valve gently convex, with maximum height near anterior margin of larval shell. Posterior margin short, straight. Pseudointerarea orthocline, forming short, narrow strip with slight median depression. Propareas absent. Cardinal muscle scars small, elongate, located near posterolateral margins. Central muscle

scars not apparent. Mantle canals not apparent. Median ridge low, extending anteriorly from pseudointerarea to between two-thirds to three-quarters of valve length.

Etymology.--Latin, *Cyclops*, one-eyed giant of Greek mythology.

Types.--Holotype, USNM 527123, ventral valve: Deadwood Formation, Black Hills, South Dakota.

Other material examined.--One hundred and sixty three ventral valves and ninety three dorsal valves from locality A, Black Hills, South Dakota.

Occurrence.--Upper Middle Cambrian (Marjuman Stage) of western Newfoundland, Canada and lower Upper Cambrian (Marjuman Stage) of South Dakota, USA.

Discussion.--*Amplitreta cyclopis* is readily distinguishable externally by its large larval shell, and high rugose ridges ornamenting the postlarval shell.

The large foramen with flange-shaped internal tube is apparent in all examined specimens, both from South Dakota and Newfoundland. This feature is due to resorption of shell material and may be variably developed in some individuals.

While *Amplitreta* is similar to *Aphelotreta*, *Amplitreta cyclopis* is also similar to the Upper Cambrian linnarssoniinaen species *Anabolatreta tegula* Rowell and Henderson, 1978 sharing a similarly shaped apical process with median groove. The dorsal valves are also very similar with respect to their narrow orthocline pseudointerareas and low median ridges. The primary differences are that *Amplitreta cyclopis* has a catacline rather than procline ventral valve, and has an

ornament of concentric rugose ridges rather than the distinctive lamellae seen in *Anabolatreta tegula*.

AMPLITRETA ELONGATA new species

Plate 7, figures 1-14

Diagnosis.--Ventral valve with incurved beak overhanging posterior margin. Foramen elongate, not contained within larval shell; length variable. Apical process low, subtriangular. Dorsal valve with very low median ridge, cardinal muscle scars minute.

Description.--Shell transversely oval in outline with ornament of fine concentric growth lines. Ventral valve gently convex, with concave posterior margin. Pseudointerarea catacline, with narrow intertrough. Beak incurved, extending beyond posterior margin. Foramen relatively large, posteriorly directed, not contained within larval shell. Foramen shape varies due to resorption from elongate subcircular to elongate oval; in some specimens, foramen completely resorbed, creating triangular delthyrium. Apical process very low, subtriangular, indistinct in some specimens. Muscle scars not apparent. Mantle canals not apparent.

Dorsal valve gently convex, with maximum height near anterior margin of larval shell. Posterior margin short, straight. Pseudointerarea orthocline, forming short, narrow strip with slight median depression. Propareas absent. Cardinal muscle scars minute, located near posterolateral margins. Central muscle scars not

apparent. Mantle canals not apparent. Median ridge extremely low, extending anteriorly from pseudointerarea to approximately two-thirds of valve length.

Etymology.--Latin, *elongatus*, prolonged.

Types.--Holotype, USNM 527129, ventral valve: Deadwood Formation, Black Hills, South Dakota. Paratypes USNM 527128, ventral valve; 527130, dorsal valve: Deadwood Formation, Black Hills, South Dakota.

Other material examined.--Twelve ventral valves and eighteen dorsal valves from locality 'B,' Black Hills, South Dakota.

Occurrence.--Lower Upper Cambrian (Marjuman Stage) of South Dakota.

Discussion.--*Amplitreta elongata* is distinguished by its low convexity and elongate foramen. In half of the specimens examined, resorption of the foramen had extended beyond the posterior margin, creating a triangular delthyrium similar to that in *Curticia*. This condition was also illustrated in *Pegmatreta rotunda* (Bell, 1941, pl. 30, fig.28), but *Amplitreta elongata* differs from *P. rotunda* in being gently convex rather than highly convex, and in having an apical process that is a low, subtriangular callosity rather than the knob-shaped, dorsally directed apical process of *P. rotunda*.

The dorsal valves of *Amplitreta elongata* are similar to those of *A. cyclopis*, but can be distinguished by the ornamentation of fine growth lines, lower median ridge and much smaller cardinal muscle scars.

ANABOLATRETA Rowell and Henderson, 1978

Type species.--*Anabolatreta tegula* Rowell and Henderson, 1978.

Other species.--*Anabolatreta* sp. (Popov, 1985); *Anabolatreta diversa* Koneva, 1986; *Anabolatreta lepida* Koneva, 1986; *Anabolatreta groenlandica* Zell and Rowell, 1988; *Anabolatreta dorsata* Mei, 1993; *Anabolatreta* sp. Popov et al., 1996; aff. *Anabolatreta tora* n. sp.

Diagnosis.--See Holmer and Popov (2000).

Occurrence.--Middle to Upper Cambrian of New South Wales and western Queensland, Australia (Boomerangian-Mindyallan stages); Kazakhstan (*Lejopyge armata-Glyptagnostus reticulatus* zones); Krygyzstan; North Greenland (*Cedaria-Aphelaspis* zones); North China (*Westergaardodina matsushitai* Zone); Siberia (*Lejopyge laevigata-Glyptagnostus stolidotus* zones); the Great Basin of Nevada and Utah, possibly the Black Hills of South Dakota, United States (*Crepicephalus-Aphelaspis* zones).

aff. ANABOLATRETA TORA new species

Plate 8, figures 6-17

Diagnosis.--Shell strongly ventribiconvex. Ventral valve conical; posterior slope straight, anterior slope concave. Apical process high, broad, with steep, well-defined anterior margin, and deep depression posteriorly, through which pedicle tube emerges. Dorsal valve gently convex. Pseudointerarea orthocline, forming undivided subtriangular shelf.

Description.--Shell circular with short, straight posterior margin; ornamented with distinctive growth lamellae.

Ventral valve conical. Pseudointerarea procline; intertrough absent. Posterior slope straight, anterior slope concave. Pedicle foramen posterior to beak, not enclosed within larval shell. Apical process high, broad, with steep, well-defined anterior margin, and deep posterior depression; occludes entire apex in some specimens. Pedicle tube long, dorsally directed, emerging through deep depression in posterior end of apical process. Apical pits large, located one either side of posterior end of apical process, anterior to pedicle tube. Muscle scars and mantle canals not apparent.

Dorsal valve subcircular with elongate beak. Pseudointerarea orthocline, undivided, forming subtriangular shelf overhanging valve floor. Median ridge very low, nearly indiscernable. Muscle scars, mantle canals not apparent.

Etymology.--Latin, *torus*, round elevation, protuberance, or bulge.

Types.--Holotype, USNM 527132, ventral valve: Deadwood Formation, Black Hills, South Dakota. Paratype, USNM 527134, dorsal valve: Deadwood Formation, Black Hills, South Dakota.

Other material examined.--Four ventral valves and one dorsal valve from locality A, Black Hills, South Dakota.

Occurrence.--Lower Upper Cambrian (Marjuman Stage) of South Dakota.

Discussion.--aff. *Anabolatreta tora* has a very distinctive apical process that is higher and broader than other species of *Anabolatreta*, and completely occludes the apex in some specimens. It is similar to *Anabolatreta dorsata* Mei, 1993 in having a more highly conical ventral valve than is normal for the genus, and having an apical process that encompasses the internal foramen. It is similar to

Anabolatreta groenlandica Zell and Rowell, 1988 in having a concave anterior slope.

The dorsal valve, however, is unlike that of any species assigned to *Anabolatreta*. It has a large, well-defined dorsal pseudointerarea, whereas the dorsal pseudointerareas of all other species of *Anabolatreta* are consistently vestigial. It also differs in being gently, rather than moderately, convex. The dorsal valve is most similar to that of *Longipegma thulensis* Popov and Holmer, 1994, but with a much lower median ridge.

The dorsal valve of aff. *Anabolatreta tora* is so dissimilar to that of the type species that assignment of this species to *Anabolatreta* is dubious despite the great similarity of the ventral valve. Either this species represents a new, though closely related, genus or the concept of *Anabolatreta* must be expanded to include a wider variation of dorsal pseudointerareas.

Genus OPISTHOTRETA Palmer, 1954

Type species.--*Opisthotreta depressa* Palmer, 1954.

Other species.--*Opisthotreta verchojanica* Pelman, 1986 (*in* Ermak and Pelman, 1986); *Opisthoteta minuta* Mei, 1993; *Opisthotreta* sp. (Holmer, Popov, and Lehnert, 1999); *Opisthotreta nuda* n.sp.

Diagnosis.--Shell nearly equibiconvex, subcircular with short posterior margin. Ventral pseudointerarea low, apsacline. Apical process expanding anteriorly, or absent. Dorsal pseudointerarea with median groove and vestigial propareas. Median ridge vestigial or absent.

Occurrence.--Upper Cambrian of Texas, South Dakota, Argentina, southeastern Siberia, and North China.

Discussion.--The diagnosis of Holmer et al. (1999) is modified slightly to incorporate *Opisthotreta nuda* n. sp., which lacks the rounded posterior margin, apical process, and dorsal sulcus, previously considered to be diagnostic characters of the genus.

OPISTHOTRETA NUDA new species

Plate 9, figures 1-13

Opisthotreta sp. ROBSON, NOWLAN AND PRATT, 2003, p. 206, figs. 5.13-5.20.

Diagnosis.--Shell subcircular with short, straight posterior margin. Ventral pseudointerarea low, apsacline, with shallow intertrough. Apical process absent. Muscle scars, mantle canals absent. Dorsal pseudointerarea vestigial, represented by short strip with shallow median depression. Median septum absent. Muscle scars and mantle canals absent.

Description.--Shell biconvex, subcircular with short, straight posterior margin. Larval shell well defined, with ornamentation of fine pits. Postlarval shell ornamented with concentric, rugose growth lines.

Ventral pseudointerarea low, strongly apsacline with broad, shallow intertrough. Pedicle foramen relatively large, posteriorly directed, extending slightly beyond posterior valve margin; contained entirely within larval shell. Apical process absent. Muscle scars and mantle canals not apparent.

Dorsal pseudointerarea vestigial, represented by short strip with shallow median depression. Beak extends to posterior margin. Median septum absent. Muscle scars and mantle canals not apparent.

Etymology--Latin *nudus*, naked, bare, or empty.

Types.--Holotype, USNM 527135, ventral valve: Deadwood Formation, Black Hills, South Dakota. Paratype, USNM 527136, conjoined shell: Deadwood Formation, Black Hills, South Dakota.

Other material examined.--Sixty three ventral valves, twenty seven dorsal valves, and seven conjoined shells from locality B, Black Hills, South Dakota.

Occurrence.--Lower Upper Cambrian (Marjuman Stage) of Alberta and South Dakota.

Discussion.--*Opisthotreta nuda* is distinguished by its lack of internal features. The specimens described here are similar to the type species in its shell shape and distinctive ventral pseudointerarea, but *Opisthotreta nuda* differs from *O. depressa* in lacking an apical process, dorsal median ridge, and cardinal muscle scars. *Opisthotreta verchojanica* differs from *O. nuda* in having a median ridge and lacking an intertrough in the ventral pseudointerarea. *Opisthotreta nuda* is most similar to specimens of *Opisthotreta* sp., from the Argentine Precordillera, described by Holmer et al. (1999). They share a short, strip-like dorsal pseudointerarea, and both lack a dorsal median septum. But the Argentinian specimens, unlike *Opisthotreta nuda*, have well-developed ventral cardinal muscle fields.

Genus STILPNOTRETA Henderson and MacKinnon, 1981

Type species.--*Stilpnotreta magna* Henderson and MacKinnon, 1981.

Other species.--*Stilpnotreta tecta* Koneva, 1990; *Stilpnotreta* sp. (Puura and Holmer, 1993); *Stilpnotreta inaequalis* Ushatinskaya, 1994; *Stilpnotreta galinae* Popov, Holmer, and Gorjansky, 1996; *Stilpnotreta minuta* Holmer, Popov, Koneva, and Basset, 2001.

Diagnosis.--See Holmer et al., 2001.

Occurrence.--Middle to Upper Cambrian; Antarctica, Australia, Canada, Great Britain, Kazakhstan, Kyrgyzstan, New Zealand, Siberia, Sweden, United States.

STILPNOTRETA MAGNA Henderson and MacKinnon, 1981

Plate 10, figures 1-11

Stilpnotreta magna HENDERSON AND MACKINNON, 1981, p. 298, figs. 7A-J, 8; HOLMER, POPOV, KONEVA, AND BASSETT, 2001, p.118, pl 34, figs. 15-18, pl. 35, figs. 1-11; ROBSON, NOWLAN AND PRATT, 2003, p. 206, figs. 6.6-6.13.

Diagnosis.--See Henderson and MacKinnon, 1981.

Description.--Shell equibiconvex, subcircular in outline. Ventral pseudointerarea apsacline, concave. Thickened apical region perforated by large internal foramen that passes into short tube, emerging as large external foramen. Beak narrow, extending beyond posterior margin. Apical process forms very low elongate, subtriangular rise. Posterolateral muscle scars elongate. Dorsal pseudointerarea orthocline with wide median groove and vestigial propareas. Low

median ridge extends from pseudointerarea to one third of valve length. Posterolateral muscle scars elongate.

Material examined.--Five ventral valves and six dorsal valves from locality 'A,' Black Hills, South Dakota.

Occurrence.--Middle to Upper Cambrian Georgina Basin, Queensland; Tasman Formation, New Zealand; Middle Cambrian Sarykumy Formation, Kazakhstan; lower Upper Cambrian (Marjuman Stage) Deadwood Formation of Alberta, Canada, and South Dakota, U.S.A.

Discussion.--Specimens of *Stilpnotreta magna* from South Dakota differ slightly from those of Alberta in having a longer beak that extends further beyond the posterior margin, a concave rather than flat ventral pseudointerarea, and a lower apical process. The dorsal valves, however, are nearly identical and the differences in the ventral valves are regarded as minor variation within the species.

Family CURTICIIDAE Walcott and Schuchert, 1908 (in Walcott, 1908)

Discussion.--Walcott and Schuchert (1908) originally placed the Curticiidae within the Obolacea. This is understandable given that the deep, narrowly triangular pedicle groove of *Curticia* is very similar to that of many obolids, such as *Dicellomus* and *Obolus*. In fact, Walcott (1912) noted that specimens of *Curticia elegantula* Walcott, 1905 were misidentified as *Dicellomus politus* Hall, 1871 by the field collector. When Rowell and Bell (1961) reassigned the family to the Acrotretida, they noted the pedicle groove is caused by resorption of shell material

around the foramen, and that the musculature is similar to that of *Linnarssonella*. Additionally, the concave plate of the dorsal pseudointerarea is reminiscent of *Linnarssonella girtyi* Walcott, 1902.

However, *Curticia* seems to be even more closely related to the Linnarssoniinae, particularly *Picnotreta* Henderson and MacKinnon, 1981. *Picnotreta* is characterized by a ventral pseudointerarea buttressed by apical thickening (see revised diagnosis in Robson and Pratt, 2001), which is perforated by a posteriorly tapering pedicle tube. The buttress seen in *Picnotreta* is virtually identical to that of *Curticia minuta* Bell (1944) and *C. pustulosa* n. sp., described below. Furthermore, the pseudointerareas of *Picnotreta robusta* Holmer, Popov, and Lehnert, 1999 and *P. lophocracenta* Robson and Pratt, 2001 feature a concave median plate bounded by narrow triangular propareas that are also nearly identical to those of *Curticia*. If the same sort of shell resorption has occurred in *Picnotreta* as in *Curticia*, the pedicle tube would resemble a narrow, triangular pedicle groove, and the entire pseudointerarea would be identical to that of *Curticia*. Furthermore the low apical process in *Curticia minuta* is similar to that of *Picnotreta lophocracenta*, while the low, anteriorly expanding apical process with the median concavity in *C. pustulosa* is nearly identical to, though more subdued than, the apical process of *Picnotreta debilis* Henderson and MacKinnon, 1981.

Genus CURTICIA Walcott, 1905

Curticia WALCOTT, 1905, p. 319, pl. 1, figs. 2, 2a-l; WALCOTT, 1908, p. 142, pl. 11; WALCOTT, 1912, p. 369, pl. 1, figs. 2, 2a-2l.

Type species.--*Curticia elegantula* Walcott, 1905.

Other species.--*Curticia minuta* Bell, 1944; *Curticia pustulosa* n. sp.

Diagnosis.--See Holmer and Popov (2000)

Occurrence.--Middle Cambrian of North Greenland. Upper Cambrian of Minnesota, Montana, South Dakota, and western Argentina.

Discussion.--Rowell and Bell (1961) re-examined the genus, applying Bell's (1948) acetic acid etching technique to specimens of *Curticia minuta*, which provided greater detail than Bell (1944) was able to achieve with mechanical preparation. Unfortunately acetic acid etching could not be applied to specimens of *Curticia elegantula* as they were preserved in dolomitic sandstone. They were, however, able to improve upon the mechanical preparation of the topotypes and obtain a greater level of detail than was previously available, allowing them to improve the description of the type species.

CURTICIA MINUTA Bell, 1944

Plate 11, figures 1-16

Curticia minuta BELL in Lochman and Duncan, 1944, p. 145, pl. 18, figs. 22-31; ROWELL AND BELL, 1961, p. 928, pl. 104, figs. 1-20; ZELL AND ROWELL, 1988, p. 140, figs. 12.1-12.8.

Diagnosis.--Larval shells pitted, postlarval shells glossy, with ornament of rugose growth lines. Ventral pseudointerarea concave, orthocline to apsacline. Propareas deflected sharply by flexure lines, ornamented with growth lines. Beak

extends slightly beyond valve margin, thickened internally. Dorsal pseudointerarea orthocline to slightly anacline, with slight pedicle groove. Beak marginal.

Description.--Shell ventribiconvex, transversely oval in outline. Larval shells pitted, postlarval shells glossy.

Ventral valve strongly convex in lateral profile; exterior smooth, with growth lines becoming more pronounced and rugose towards anterior margin. Pseudointerarea concave, procline to apsacline, divided into propareas by triangular pedicle groove. Propareas connected by thin ridge or groove at apex (Pl. 11, fig. 5), ornamented with growth lines running parallel to base of pseudointerarea. Beak slightly overhangs posterior margin, thickened internally forming buttress. Apical pits located at base of pedicle groove. Low apical process extends from base of buttress to approximately one-quarter of valve length. Posterolateral muscle scars small, located at base of propareas near lateral margins. *Vascula lateralia* extend anteriorly from apical pits to approximately one-third of valve length.

Dorsal valve very gently concave in lateral profile; external ornamentation of rugose growth lines. Pseudointerarea orthocline to slightly anacline with broad, triangular plate extending from beak forming shallow shelf, and slight pedicle groove. Beak marginal. Low median ridge extends from base of pseudointerarea to two-thirds of valve length. Posterolateral muscle scars large, oval, located at base of pseudointerarea on either side of median ridge.

Material examined.--Sixteen ventral valves and twenty one dorsal valves from locality B, Black Hills, South Dakota.

Occurrence.--Lower Upper Cambrian (Marjuman Stage) of Montana and South Dakota.

Discussion.--The specimens described here accord, in most respects, with the description of *Curticia minuta* given by Rowell and Bell (1961). The only differences noted are that the specimens from the Deadwood Formation have pitted larval shells, as is characteristic of the Acrotretida, while Rowell and Bell (1961) reported that there were no punctae or pits in their specimens. They also reported two sets of muscle scars in the ventral valve, and the specimens described here appear to have only a single pair of posterolateral muscle scars. Lastly, the ventral valves of our specimens have a very low apical process in the ventral valve, which was not reported in the specimens of *Curticia minuta* described by Rowell and Zell (1961), although this feature is indistinct and difficult to see in many specimens.

Though a diagnosis of the species has not been given previously, Rowell and Bell (1961) noted that the most readily apparent difference distinguishing *Curticia minuta* from *C. elegantula* was its much smaller size, on average, and its thinner shell. The other features unique to *Curticia minuta* are its marginal beak in both the ventral and dorsal valves, and the internal buttressing of the ventral pseudointerarea. its orthocline to apsacline ventral pseudointerarea also creates a lower profile than seen in *Curticia elegantula*, which has an apsacline to catacline profile.

It has been pointed out that there is a great deal of variability in the structure of the ventral pseudointerarea, particularly the size and shape of the pedicle groove, among specimens of *Curticia minuta* (Rowell and Bell, 1961; Zell and Rowell, 1988), and that is also the case with the Deadwood specimens. This variability may

be related to vagaries of resorption of shell material around the pedicle foramen of the juveniles.

CURTICIA PUSTULOSA new species

Plate 12, figures 1-16

Diagnosis.--Larval shell pitted, postlarval shell pustulose. Ventral and dorsal beaks overhang posterior margins. Ventral pseudointerarea apsacline to catacline with deep; pedicle groove narrow; propareas triangular, concave. Dorsal pseudointerarea orthocline to apsacline with narrow concave plate and narrow, triangular propareas.

Description.-- Shell ventribiconvex, transversely oval in outline. Larval shell pitted. Postlarval shell pustulose, ornamented with widely spaced growth lines.

Ventral pseudointerarea apsacline to catacline, partially thickened internally. Propareas narrow, triangular; median plate shallowly concave, bisected by deep pedicle groove. Beak overhangs posterior valve margin. Cardinal muscle scars small, circular, located near posterolateral margins just anterior to base of pseudointerarea. Apical pits located at base of pseudointerarea near posterolateral margins. Apical process low, indistinct, widening anteriorly, with shallow median concavity. Mantle canals not apparent.

Dorsal pseudointerarea orthocline to apsacline; short, narrow concave median plate bounded by narrow, triangular propareas. Beak extends slightly beyond posterior valve margin. Low median ridge extends from base of

pseudointerarea to approximately four-fifths of valve length. Cardinal muscle scars small, circular, located near lateral margins. Mantle canals not apparent.

Etymology.--Latin, *pustulosus*, full of blisters.

Types.--Holotype, USNM 527150, ventral valve: Deadwood Formation, Black Hills, South Dakota.

Other material examined.--Twenty four ventral valves and fourteen dorsal valves from locality A, Black Hills, South Dakota.

Occurrence.--Lower Upper Cambrian (Marjuman Stage) of South Dakota.

Discussion.--The most obvious distinguishing characteristic of *Curticia pustulosa* is its pustulose postlarval shell, appearing as a coarse, matte texture on the shell exterior, as opposed to the glossy exterior of *C. minuta*. *Curticia pustulosa* further differs from *C. minuta* in its more conical profile created by its apsacline to catacline pseudointerarea, by its ventral and dorsal beaks, which overhang the posterior margins, and by its much deeper pedicle groove in the ventral valve. Furthermore, the internal thickening of the beak is more substantial in *Curticia minuta*, creating a more robust buttress of the pseudointerarea.

Curticia pustulosa is more similar to *C. elegantula*, sharing several characteristics, including the inclination of the ventral pseudointerareas, and the overhanging beaks. It is distinguished from *C. elegantula* by the smaller size and thinness of the shell, the external ornament of relatively thick, widely spaced, rather than fine growth lines, the lack of radial lines in the valve interiors, and a longer dorsal median ridge, which never extends beyond one-half of valve length in *C. elegantula*.

Family SCAPHELASMATIDAE Rowell, 1965

Diagnosis.--Shell biconvex to concavo-convex with straight or slightly concave posterior margin. External ornament of regularly spaced rugae, becoming lamellose towards margins. Ventral pseudointerarea with intertrough. External foramen not completely contained within larval shell. Apical process low or absent, typically anterior to foramen. Apical pits small, lateral to apical process. Dorsal valve with or without triangular septum or low median ridge.

Discussion.--The diagnosis of Holmer and Popov (2000) is modified slightly to include a low dorsal median ridge, which is present in three of the six genera assigned to the Scaphelasmatidae.

EOSCAPHELASMA Koneva, Popov, and Ushatinskaya, 1990

Type species.--*Eoscaphelasma satpakensis* Koneva, Popov, and Ushatinskaya, 1990 (in Koneva et al., 1990).

Other species.--*Eoscaphelasma*? *delicata* Holmer, Popov, Koneva, and Basset, 2001.

Diagnosis.--See Holmer and Popov (2000).

Occurrence.--Upper Cambrian of Kazakhstan and lower Upper Cambrian (Marjuman Stage) of South Dakota.

Discussion.--*Eoscaphelasma* is very similar to, and may be congeneric with, *Kotylotreta* Koneva, 1990. The only feature that distinguishes them is that *Eoscaphelasma* has a vestigial apical process, and an elongate pedicle foramen,

while *Kotylotreta* has a low, subtriangular apical process and a circular foramen. Popov and Holmer (1994) claimed that *Eoscaphelasma* differed from *Kotylotreta* in having rugose ornamentation, a pedicle foramen not contained within the larval shell, and a short internal pedicle tube. However, an internal pedicle tube is not found in all specimens of *Eoscaphelasma* (Popov and Holmer, 1994; Holmer et al., 2001), and *Kotylotreta* also has rugose ornamentation and a pedicle foramen not contained within the larval shell. This leaves little to distinguish between them, and it is uncertain whether the vestigial apical process and elongate foramen have consistent fidelity as diagnostic characters, although specimens from South Dakota do exhibit these features.

EOSCAPHELASMA cf. SATPAKENSIS Koneva, Popov, and Ushatinskaya, 1990

Plate 8, figures 1-5

cf. *Eoscaphelasma satpakensis* KONEVA, POPOV, AND USHATINSKAYA, 1990, *in* Koneva et al., 1990, p. 165, pl. 30, figs. 1-7; POPOV AND HOLMER, 1994, p. 137, fig. 109.

cf. *Eoscaphelasma* cf. *satpakensis* (Koneva, Popov, and Ushatinskaya, 1990) HOLMER, POPOV, KONEVA, AND BASSET, 2001, p. 140, pl. 44, figs. 3-8.

Description.--Ventral valve transversely oval with ornament of fine rugae. Pseudointerarea procline with wide intertrough. Profile low conical with maximum height just posterior to mid length. Pedicle foramen relatively large, elongate, not

contained within larval shell. Apical process poorly defined, perforated by foramen. Interior otherwise featureless.

Material examined.--Three ventral valves from locality B, Black Hills, South Dakota.

Occurrence.--Upper Cambrian of Kazakhstan and lower Upper Cambrian (Marjuman Stage) of South Dakota.

Discussion.--The Deadwood Formation specimens are similar to those of *Eoscaphelasma* cf. *satpakensis* Holmer, Popov, Koneva, and Bassett (2001) from the Malyi Karatau in that they lack an internal pedicle tube. They conform in all other respects to the type species.

KOTYLOTRETA Koneva, 1990

Type species.--*Kotylotreta undata* Koneva, 1990.

Other species.--*Kotylotreta nupera* n. sp.

Diagnosis.--Shell transversely oval with ornament of fine growth filae, sometimes with widely spaced rugae. Ventral valve low, conical. Pseudointerarea procline with shallow intertrough. Foramen not contained within larval shell. Apical process extends between anterior and posterior slopes, perforated by internal foramen. Apical pits weakly impressed, located lateral to foramen. Dorsal valve pseudointerarea vestigial with broad, shallow median groove. Median ridge low.

Occurrence.--Middle Cambrian of Malyi Karatau and Kyrgyzstan. Upper Cambrian of the United States.

Discussion.--The diagnosis of Holmer et al. (2001), is modified slightly to incorporate *Kotylotreta nupera* n. sp. Holmer et al. (2001) reassigned *Kotylotreta* from the Acrotretidae to the Scaphelasmatidae, citing its similarity to *Eoscaphelasma* and distinguishing it from the latter by its broadly triangular apical process and lack of growth lamellae. *Kotylotreta nupera* n. sp. has peripheral growth lamellae similar to that of *Eoscaphelasma*, so the apical process is the only feature by which the two genera can be distinguished. It may be argued that *Kotylotreta* and *Eoscaphelasma* are synonymous, much as Holmer et al. (2001) considered *Pegmatreta* Bell, 1941 to be a junior synonym of *Linnarssonia* Walcott, 1885 based on its lower apical process and unthickened muscle scars. Given that *Kotylotreta* and *Eoscaphelasma* were each previously known from only one definite species, it is premature to confirm whether or not they are synonymous and are treated here as two distinct genera.

KOTYLOTRETA UNDATA Koneva, 1990

Plate 13, figures 15-17

Kotylotreta undata KONEVA, 1990, p. 50, pl. 5, figs. 9-17; HOLMER, POPOV, KONEVA, AND BASSETT, 2001, p. 146, pl. 45, figs. 1-14, pl. 46, figs. 1-5, 7.

Diagnosis.--Shell with ornament of fila. Ventral valve low, conical. Apical process broad, subtriangular, with base on anterior slope, tapering on posterior slope, perforated at apex by large internal foramen. Dorsal valve gently convex. Median ridge low or absent.

Description.--Ventral valve transversely oval, with ornament of fila. Pseudointerarea procline, with shallow intertrough. Profile low conical, with maximum height at one-third of valve length from posterior margin. Pedicle foramen not contained within larval shell. Apical process subtriangular with base on anterior slope, tapering on posterior slope, perforated at apex by large internal foramen. Apical pits, muscle scars, mantle canals not apparent.

Material examined.--Two ventral valves from locality 'B,' Black Hills, South Dakota.

Occurrence.--Middle Cambrian of Kazakhstan, Kyrgyzstan, and possibly New South Wales, Australia. Lower Upper Cambrian (Marjuman Stage) of South Dakota, United States.

Discussion.--The ventral valves described here are identical to specimen illustrated by Holmer et al. (2000, pl. 45, fig. 5).

KOTYLOTRETA NUPERA new species

Plate 13, figures 1-14

Diagnosis.--Ventral valve conical with gently convex anterior and posterior slopes. Maximum height just posterior of mid length. Apical process long, triangular on anterior slope, tapering posteriorly to internal foramen; continuing as narrow ridge on posterior slope. Dorsal valve convex in umbonal region, becoming flat peripherally.

Description.--Shell ventribiconvex, transversely oval in outline, with ornament of rugose, growth lamellae.

Ventral valve conical with maximum height just posterior of midline; anterior and posterior slopes gently convex. Pseudointerarea procline, with shallow, poorly defined intertrough. Posterior margin concave. External foramen small, circular, posteroventrally directed, not contained within larval shell. Apical process low, broad, triangular, with acutely tapering apex leading to internal foramen, continuing as a narrow ridge on the posterior wall. Apical pits small, weakly impressed, located on either side of apical process near internal foramen. Cardinal muscle scars small, elongate located on posterolateral slopes. *Vascula lateralia* weakly impressed, short, extending along each side of apical process.

Dorsal valve gently convex with maximum height in umbonal region. Posterior margin short, straight. Beak marginal. Psuedointerarea short, orthocline, with broad, low triangular median plate bordered by minute acutely triangular propareas. Median ridge low, extending anteriorly from pseudointerarea to three-quarters of valve length. Two short mediolateral ridges on either side of median ridge. Cardinal muscle scars small, located near posterolateral valve margins.

Etymology.--Latin, *nuperus*, new, recent, late.

Types.--Holotype, USNM 527161, ventral valve: Deadwood Formation, Black Hills, South Dakota.

Other material examined.--Fourteen ventral valves and five dorsal valves from locality B, Black Hills, South Dakota.

Occurrence.--Lower Upper Cambrian (Marjuman Stage) of South Dakota.

Discussion.--*Kotylotreta nupera* can be distinguished from the type species by its elongate triangular process tapering posteriorly to the internal foramen, and

by the lateral profile of the dorsal valve, which is convex in the umbonal region, then flattening towards the margins. It is similar to *Anabolatreta tegula* Rowell and Henderson, 1978, sharing a very similar apical process and dorsal valve whose interior differs only in having a straight posterior margin.

Order LINGULIDA Waagen, 1885

Family OBOLIDAE King, 1846

Genus DICELLOMUS Hall, 1871

Type species.--*Lingula polita* Hall, 1861.

Other species.--*Dicellomus nanus* Meek and Hayden, 1862; *Dicellomus pectenoides* Whitfield, 1875; *Dicellomus appalachia* Walcott, 1905; ?*Dicellomus parvus* Walcott, 1905; ?*Dicellomus prolificus* Walcott, 1908; *Dicellomus fiestus* Lochman, 1940; *Dicellomus walcotti* Lochman, 1940; *Dicellomus mosaica* Bell, 1941; *Dicellomus amblia* Bell, 1944.

Diagnosis.--see Holmer and Popov (2000).

Occurrence.--?Middle Cambrian of China. Upper Cambrian (Marjuman Stage) of the United States and Canada.

Discussion.--Bell (1944) considered *Dicellomus* to be an index to the early Late Cambrian *Cedaria* and *Crepicephalus* zones in the United States, and thus felt that *D. parvus* Walcott, 1905, and *D. prolificus* Walcott, 1908, both Middle Cambrian species, probably did not belong to *Dicellomus*. Walcott's descriptions of these species, however, do conform to the diagnosis of the genus, and Bell (1944) provided no evidence of morphological disparity that would exclude them from the

group. A re-examination of the type material of these species should be made to determine if they belong to *Dicellomus* and whether or not the genus can truly be considered diagnostic of an early Late Cambrian age.

Most of the species of *Dicellomus* have been described as being similar to ***D. politus***, except for certain features, which, in some cases, are ambiguous. Since the type species is not well understood, this makes the validity of other species of the genus suspect. The diagnoses for the species of *Dicellomus* described below list the features which distinguish them, based on a refinement of ***D. politus*** from the Deadwood Formation. This is a temporary measure that will suffice until the type species is reexamined and more thoroughly described.

DICELLOMUS POLITUS Hall, 1871

Plate 14, figures 1-7

Obolus appolinus (Owen, 1852) OWEN, 1852, p. 576, pl. 1., figs. 9, 11, 15, 20.

Lingula polita (Hall, 1861) HALL, 1861, p. 24; WHITFIELD, 1862, p. 136.

Obolella sp. 3 BILLINGS, 1861a, p.7; BILLINGS 1861b, p. 946.

Lingula? *polita* (Hall, 1861) HALL, 1862, p. 435, fig. 1.

Obolella polita (Hall, 1861) BILLINGS, 1862b, p. 241; WHITFIELD, 1880, p. 339, pl. 2, figs. 12-13; WALCOTT, 1886, p.111; HALL AND CLARKE, 1892, p. 72, pl. 2, figs. 37-41.

Obolella? *polita* (Hall, 1861) HALL, 1863, p. 133, pl. 4, figs. 17-21; HALL, 1867, p. 112, pl. 1, figs. 17-21.

Lingulepis prima (Meek and Hayden, 1865) MEEK AND HAYDEN, 1865, p. 3, pl. 1, figs. 2a-b.

Dicellomus polita (Hall, 1861) HALL, 1871, p. 3; HALL, 1873, p. 246.

Dicellomus politus (Hall, 1861) WALCOTT, 1899, p. 443, 446, pl. 60, figs. 4, 4a, WALCOTT, 1905, p. 313; GRABAU AND SHIMER, 1907, p. 189, fig. 224; WALCOTT, 1912, p. 575, fig. 49, pl. 52, figs. 1, 1a-k, 2, 2a-i, 3, 4, 5, 5a-b; LOCHMAN, 1940, p. 19, pl. 1, fig. 8.

Diagnosis.--Shell biconvex, subtriangular in outline. Ventral pseudointerarea anacline with parallel-sided intertrough. Propareas long, narrow with articulatory socket. Visceral area spatulate, expanding anteriorly, with central depression. Posterolateral muscle scars large, oval. Dorsal pseudointerarea apsacline with shallow median depression. Propareas narrow with articulatory ridge. Posterolateral muscle scars large, oval. Median muscle scars small, circular, located on either side of short, low median ridge, near anterocentral margin of posterolateral muscle scars.

Description.--Shell biconvex; valves thick, with especially thickened visceral areas.

Ventral valve transversely subtriangular with maximum width near anterior margin. Pseudointerarea anacline; intertrough with nearly parallel sides; propareas long, narrow, with articulatory grooves along posterior half; flexure lines well developed. Visceral area spatulate, expanding anteriorly to one-half valve length, thickened. Posterolateral muscle scars large, oval, positioned approximately one-quarter of valve length from apex. *Vascula lateralia* straight, extending along inside

edge of muscle scars to three quarters of valve length from apex. Valve floor coarsely pitted.

Dorsal valve transversely oval to subtriangular with maximum width anterior of midline. Pseudointerarea apsacline with shallow median depression. Proparеareas narrow with articulatory ridge. Beak marginal. Median ridge short, low, located at midpoint of valve. Posterolateral muscle scars large, oval. Central muscle scars small, circular, located on either side of median ridge near anteromedial margins of posterolateral muscle scars. Valve floor pitted.

Material examined.--Fourteen dorsal valves and twelve ventral valves from locality B, Black Hills, South Dakota.

Occurrence.--Lower Upper Cambrian (Marjuman Stage) of Arizona, Minnesota, Missouri, Montana, Oklahoma, South Dakota, Tennessee, Utah, and Wisconsin.

Discussion.--*Dicellomus politus* is poorly understood, known mainly from shell exteriors and occasional internal molds, recovered from sandstones and shales. Many of the internal features of the species described by Walcott (1912), such as the rudimentary pedicle tube and "cardinal margins," are artifacts of poor preservation. The specimens described here, obtained from limestone by acetic acid digestion, are better preserved and demonstrate the diagnostic features better than most that have been previously described. One of the most prominent diagnostic characters of *Dicellomus politus* is the presence of ridge and socket valve articulation, which was described by Walcott (1912). This feature was regarded as suspect by Bell (1941), but is clearly present in every specimen examined here, and is similar to the

articulatory structures found in *Linnarssonella* as illustrated by Robson et al. (2003, figs. 3.5, 3.9-3.11, and 4.5-4.7).

It is likely that many specimens referred in the past to *Dicellomus politus* do not belong to this species, and a thorough reexamination of the type material is necessary to clearly define the species. While the diagnosis of the genus (Holmer and Popov, 2000) is unambiguous, until the type species is better understood, the diagnoses of all other species referred to the genus are suspect since many of them are described as being "similar to *Dicellomus politus*, except..." The diagnosis of *Dicellomus politus* given above is based only upon the specimens described in this study, not on the type material, which was not examined, and therefore may not be a true representation of the distinguishing features of the species.

DICELLOMUS cf. AMBLIA Bell, 1944

Plate 15, figures 7-10

Dicellomus amblia BELL, 1944, p. 149, pl. 19, figs. 1-4; LOCHMAN, 1964, p. 42, pl. 9, figs. 13-19.

Dicellomus ?*amblia* (Bell, 1944) HOLMER AND POPOV, 2000, p. 45, fig. 15, 3a-h.

Diagnosis.--Shell transversly subtrigonal; biconvex to ventribiconvex. Ventral visceral area coarsely pitted. Dorsal beak blunt, incurved at apex, extending beyond posterior valve margin.

Description.--Shell ventribiconvex, transversely subtriangular in outline. Ventral pseudointerara strongly anacline, with pedicle groove forming narrow median depression; propareas form articulatory ridges. Posterolateral muscle scars large, elongate. Visceral area thickened anteriorly. Valve floor coarsely endopunctate.

Dorsal pseudointerarea vestigial, with propareas forming articulatory ridges and grooves. Median ridge not apparent. Posterolateral muscle scars large, oval, central muscles scars weakly impressed. Valve floor coarsely endopunctate.

Material examined.--Nine ventral and nineteen dorsal valves from locality A, and B, Black Hills, South Dakota.

Occurrence.--Lower Upper Cambrian (Marjuman Stage) of South Dakota and Montana.

Discussion.--The assignment of the specimens described here to *D. amblia* is provisional because the beak of the dorsal valve does not protrude far beyond the posterior valve margin, nor is it as strongly incurved as the specimens described by Bell (1944). They conform in all other respects to *Dicellomus amblia*, particularly in size, outline, convexity, and the coarse pitting of the visceral area.

DICELLOMUS APPALACHIA Walcott, 1905

Plate 15, figures 11-14

Dicellomus appalachia WALCOTT, 1905, p. 314; WALCOTT, 1912, p.572, pl. 53, fig. 4; LOCHMAN, 1940, p.18, pl. 1, figs. 9-12.

Dicellomus occidentalis BELL, 1941, p. 218, pl. 29, figs. 18-23; BELL, 1944, p. 149, pl. 19, figs. 6-21; LOCHMAN, 1964, p. 42, pl. 9, figs. 1-4.

Diagnosis.--Shell subtrigonal to oval, dorsibiconvex. Ventral propareas large. Pedicle groove deep, triangular. Visceral area spatulate, extending one-half of valve length. Anterior half of valve interior with radial furrows. Dorsal central muscle scars nearly in contact with minute anterolateral scars.

Description.--Ventral valve trigonal; length equal to width, with maximum width approximately two-thirds of valve length from apex. Pedicle groove deep, triangular, bounded by large, triangular propareas extending approximately one-quarter valve length from apex. Visceral area thickened, spatulate, extending one-half of valve length from apex, with shallow central depression. Posterolateral muscle scars large, elongate; central muscle scars small, circular. *Vascula lateralia* arcuate, curving inward in anterior half of valve. Anterior half of valve with radial furrows, most prominent around anterior margin.

Material examined.--Six ventral valves from locality B, Black Hills, South Dakota.

Occurrence.--Lower Upper Cambrian (Marjuman Stage) of Alabama, Missouri, South Dakota, Tennessee, and possibly Montana.

Discussion.--*Dicellomus occidentalis* Bell, 1941 was described as being very similar to *D. appalachia*, distinguished from the former by its larger size (6-7 mm in diameter compared with *D. appalachia*'s average size of 4 mm), a "somewhat different arrangement of dorsal and ventral pallial sinuses," and smaller, more numerous punctae in the inner shell layers. Lochman (1964) reported *Dicellomus*

occidentalis from the subsurface Deadwood Formation of Montana, and noted that it ranged in size from 1 mm to 7 mm. Thus the only significant distinguishing characteristic appears not to be valid, and the other features mentioned by Bell (1941) are vague. Therefore we consider *Dicellomus occidentalis* to be a junior synonym of *D. appalachia*.

DICELLOMUS NANUS Meek and Hayden, 1862

Plate 16, figures 1-11

Obolella nana MEEK AND HAYDEN, 1862, p. 435; HAYDEN, 1862, p. 73, figs. 1a-b, 2a-b; BILLINGS, 1862, p. 67; MEEK AND HAYDEN, 1865, p. 4, pl.1, figs. 3a-d; WHITFIELD, 1880, p. 340, pl. 2, figs. 14-17; WALCOTT, 1886, p. 111; HALL AND CLARKE, 1892c, p. 69.

Dicellomus nanus (Meek and Hayden, 1862) WALCOTT, 1899, p. 447, pl. 60, figs. 3a-d (not fig. 3); WALCOTT, 1905, p. 314; WALCOTT, 1912, p. 573, pl. 53, figs. 1, 1a-1, 2, 2a, 3, 3a-d; LOCHMAN, 1938, p. 470, pl. 57, figs. 1-3.

Diagnosis.--Shell transversely subtriangular to transversely oval; deeply dorsibiconvex. Ventral beak acuminate, extending beyond posterior margin. Pseudointerarea short, anacline, divided by shallow pedicle groove; propareas with articulatory groove on lateral margins; flexure lines absent. Posterolateral muscle scars large. Visceral area short, not extending to mid length. Dorsal pseudointerarea short, apsacline; propareas form articulatory ridge on lateral margins. Beak extends slightly beyond posterior margin. Posterolateral muscle scars large. Median ridge short.

Description.--Shell transversely subtriangular to transversely oval; deeply dorsibiconvex. Ventral beak acuminate, extending beyond valve margin; pseudointerarea short, anacline, divided by shallow pedicle groove; propareas long, thin, extending one-quarter to two-thirds of valve length from apex, with articulatory groove on lateral margins. Posterolateral muscle scars large, elongate. *Vascula lateralia* extend along inner edge of posterolateral muscle scars to three-quarters of valve length from apex. Visceral area spatulate, weakly thickened, short, extending to less than one-half of valve length from apex; visceral field endopunctate. Anterior third of valve with radial furrows. Valve width approximately equal to length.

Dorsal pseudointerarea short, undivided, apsacline; propareas narrow, forming articulatory ridge. Beak extends slightly beyond posterior margin. Visceral area thickened, short, extending to less than one-half of valve length from apex. Median ridge narrow, short, less than one-third of valve length. Posterolateral muscle scars large, elongate, deeply incised. Central muscle scars small, shallowly impressed, located on either side of median ridge. *Vascula media* diverge anteriorly from median ridge; *vascula lateralia* not apparent. Valve wider than long; coarsely endopunctate. Radial furrows evident along anterior margin.

Material examined.--Sixty-nine dorsal and six ventral valves from locality B, Black Hills, South Dakota.

Occurrence.--Lower Upper Cambrian (Marjuman Stage) of Wyoming, Montana, South Dakota, and western Newfoundland; Ordovician of Wyoming.

Discussion.--*Dicellomus nanus* is similar to *D. politus* in its subtriangular outline, large posterolateral muscle scars, and the articulatory ridge and sockets found on the dorsal and ventral propareas. The ventral valve differs from that of *Dicellomus politus* (as based on specimens from the Deadwood Formation) in having a thinner shell, an acuminate ventral beak that extends well beyond the posterior margin, and a shorter visceral area. It has a shallow pedicle groove unbounded by margins, and lacks flexure lines, unlike *Dicellomus politus*, which has a more rounded marginal beak with a deep pedicle groove bounded by parallel margins, and well-developed flexure lines. The dorsal valves of *Dicellomus nanus* and *D. politus* are more difficult to tell apart, but *D. nanus* has a much thinner shell and a beak that extends slightly beyond the posterior margin, rather than the marginal beak of *D. politus*.

Walcott (1912) noted that *Dicellomus nanus* was essentially the same as *D. politus*, differing primarily in shell outline and convexity. Lochman (1938) described the deep convexity of the valves as being particularly characteristic of the species, but this feature is only prominent in large, fully grown specimens. The specimens from the Deadwood Formation range from 1 mm to 4 mm in diameter, and it is only in the larger specimens (> 2mm) that the particularly deep convexity is well developed.

DICELLOMUS aff. PARVUS Walcott, 1905

Plate 15, figures 1-6

?*Dicellomus parvus* WALCOTT, 1905, p. 315; WALCOTT, 1912, p. 574, pl. 89, fig. 11; WALCOTT, 1913, p. 71, pl.3, fig. 3.

Diagnosis.--Shell transversely oval to subcircular; thin; small for genus, averaging approximately 1.5 mm in diameter. Dorsal valve shallowly convex, with maximum convexity in posterior one-third of valve. Umbo blunt, incurved, extending beyond posterior valve margin.

Description.--Shell transversely oval to subcircular in outline. Dorsal valves small; thin; shallowly convex, with maximum convexity in posterior one-third of valve. Umbo blunt, incurved, extending beyond posterior margin of valve. Pseudointerarea vestigial. Median ridge thin, low, extending from posterior margin to just past midlength of valve. Posterolateral muscle scars large, well-defined. Central muscle scars shallow, indistinct. Valve floor sparsely punctuate.

Material examined.--Twelve dorsal valves from locality B, Black Hills, South Dakota.

Occurrence.--Lower Upper Cambrian (Marjuman Stage) of South Dakota and, possibly, Middle Cambrian of Shan-tung, China.

Discussion.--*Dicellomus parvus* Walcott, 1905 is known only from the Middle Cambrian Kiulung Group of China. Bell (1944) suggested that this species probably does not belong to *Dicellomus*, and though he gave no argument to support this exclusion, the fact that *Dicellomus* is regarded as endemic to the early Late Cambrian of North America is perhaps reason enough to question *D. parvus*'s taxonomic status. The specimens assigned here to *Dicellomus* aff. *parvus* may represent a new species and, although only twelve dorsal valves have been

identified, they share many characteristics with *Dicellomus parvus*, including overall shell shape, low convexity, small size and thinness of the shell. The largest specimen of *Dicellomus parvus* is 2.5 mm long and 2mm wide, which compares favorably with *D.* aff. *parvus*, whose largest specimen is 2 mm long and 2.2 mm wide. This consistently small size is unusual for *Dicellomus*, which tends to have average shell sizes of 5 to 6 mm.

Dicellomus aff. *parvus*, in common with *D. amblia* Bell, 1944, shares a blunt, incurved dorsal beak that extends posteriorly beyond the valve margin, but differs in its transversely oval rather than subtriangular outline, lower convexity, and smaller size.

DICELLOMUS sp.

Plate 14, figures 12-16

Description.--Shell dorsibiconvex, oval in outline. Ventral valve elongate oval with bluntly rounded apex. Pseudointerarea anacline with narrow propareas. Visceral area not obviously thickened. Posterolateral muscle scars small. *Vascula lateralia* long, slightly arcuate.

Dorsal valve transversely oval to subrectangular. Beak extends slightly beyond posterior margin. Pseudointerarea vestigial, with shallow median depression. Median ridge short, low, located at midline. Posterolateral muscle scars small, oval, located near posterior margin. Central muscle scars elongate, located on either side of median ridge. Anterolateral muscle scars small, circular, located just anterior to central muscle scars along outside edge of the *vascula media*.

Vascula lateralia extending to mid length of valve, slightly arcuate. *Vascula media* diverge anteriorly from anterior end of median ridge.

Material examined.--Twenty-nine dorsal and two ventral valves from locality B, Black Hills, South Dakota.

Occurrence.--Lower Upper Cambrian (Marjuman Stage) of South Dakota.

Discussion.--*Dicellomus* sp. differs from the type species in its oval rather than triangular outline and thinner shell. It also lacks articulatory structures on the propareas, has small, rather than large, posterolateral muscle scars, and slightly arcuate, rather than straight, *vascula lateralia*. The ventral valve lacks a thickened, spatulate shaped visceral area characteristic of *Dicellomus politus*. The dorsal valve differs from the type species in having elongate, rather than circular, muscle scars.

Dicellomus sp. is unlike any other described species and may represent a new species but due to an insufficient number of well preserved ventral valves, and the current ambiguity in the diagnosis of the type species, one is not formally established.

Genus LINGULELLA Salter, 1866

Type species.--*Lingulella davisii* M'Coy, 1851.

Diagnosis.--See Sutton et al., 2000.

Discussion.--The type species of *Lingulella* has, until recently, been poorly understood due to lack of detailed morphological information. Consequently, *Lingulella*, as noted by Krause and Rowell (1975), has long been used as a convenient repository for nearly any elongate, smooth-shelled obolid. An enormous

number of species have been erected within the genus, and Walcott (1912) described no less than eighty-seven species. Many species were based on very minor distinctions that can easily be attributed to intraspecific variation, and there are likely many synonyms. Sutton et al. (1999, 2000) undertook a detailed reexamination of the type species, *Lingulella davisii*, and refined the diagnosis of the genus, which differs from the previous versions (e.g. Rowell, 1965; Holmer and Popov, 2000) in stressing the importance of deeply pitted interiors and well-defined flexure lines in both the ventral and dorsal valves. However, this emphasis appears overstated because deep pitting and strong flexure lines are characters that can be expected to vary somewhat among shells in different stages of development and, indeed, the strength of the internal pitting of *Lingulella similis* from the Deadwood Formation is shown to vary considerably between specimens. While we adopt Sutton et al.'s (2000) concept of *Lingulella* herein, internal pitting and flexure lines are considered diagnostic so long as they are evident in both valves.

Sutton et al.'s (2000) new diagnosis of *Lingulella* excluded many of the species previously considered to belong to the genus because, as Krause and Rowell (1975) noted, the pitting in *Linguellela davisii* "is not commonly seen in most species referred to the genus." This refined diagnosis of *Lingulella* is an important first step in revising what has hitherto been a problematic taxon, but it has also orphaned many morphologically legitimately recognized species. A re-examination of the species referred to *Lingulella* will need to be undertaken, and new genera erected to contain them.

LINGULELLA SIMILIS Walcott, 1898

Plate 17, figures 1-4

Obolus similis WALCOTT, 1898, p. 415.

Lingulella similis (Walcott, 1898) WALCOTT, 1912, p. 532, pl. 21, figs. 2, 2a-j, 3, 3a-d.

Lingulella? *incurvata* POPOV, HOLMER, AND MILLER, 2002, p. 218, figs. 4.1-4.11.

Diagnosis.--Shell elongate oval; ventral valve subacuminate, dorsal valve rounded ovate in outline. Narrow limbus surrounds anterior two-thirds of valve margins. Propareas barely raised above valve floor; flexure lines located near lateral margins. Average length-to-width ratio of 1.4. Ventral *vascula lateralia* short, extending from propareas to one-third of valve length from apex.

Description.--Shell elongate oval; external ornament of concentric growth lines; valve interiors with radial striae extending from visceral area to anterior margin; narrow limbus in anterior two thirds of valve margins; length-to-width ratio varies from 1.2 to 1.8, averaging 1.4. Visceral areas variably pitted.

Ventral apex subacuminate. Pseudointerarea anacline, barely raised above valve floor, bisected by triangular pedicle groove. Propareas large, triangular, extending one quarter of valve length from apex, with weakly developed flexure lines near lateral margins. *Vascula lateralia* short, extending from propareas to one third valve length from apex along lateral valve walls. Muscle scars not apparent.

Dorsal valve ovate with rounded apex. Pseudointerarea short, anacline, barely raised above valve floor, with shallow median depression. Propareas short, flexure lines weakly developed, located near lateral margins.

Material examined.--Eight ventral and twenty-one dorsal valves from locality B, Black Hills, South Dakota.

Occurrence.--Middle Cambrian of Nevada, Colorado, South Dakota, Missouri, Tennessee, Alabama, and Georgia. Upper Cambrian of Oklahoma, Wisconsin, Minnesota, and South Dakota.

Discussion.--Although Walcott's (1912) description of *Lingulella similis* is vague and lacks distinctive characteristics that distinguish it from other species, the specimens described here match his illustrations of *L. similis* (Walcott, 1912, plate 21, figures 2, 2a-j, 3, 3a-d) closely. Walcott (1912) also reported *Lingulella similis* co-occuring with *Dicellomus nanus* in the Black Hills of South Dakota, a relationship confirmed in this study. The specimens described here are therefore assigned with confidence to this species. These specimens are also so nearly identical to *Lingulella*? *incurvata* Popov, Holmer, and Miller,2002 from Utah that they are considered synonymous.

Lingulella similis has weakly developed flexure lines and variable internal pitting in both valves, variation that does not correspond completely to Sutton, et al.'s (2000) diagnosis, but is acknowledged to be a function of the inevitable intra- and interspecific variation.

Genus LINGULEPIS Hall, 1863

Type species.--*Lingulella acuminata* Conrad, 1839.

Other species.--*Lingulepis eros* Walcott, 1905; *Lingulepis exigua* Matthew, 1903; *Lingulepis gregwa* Matthew, 1899; *Lingulepis longinervis* Matthew, 1903; *Lingulepis nabis* Walcott, 1924; *Lingulepis pinnaformis* Owen, 1852; *Lingulepis pumila* Matthew, 1903; *Lingulepis pygmaea* Salter, 1865; *Lingulepi, roberti* Matthew, 1895; *Lingulepis rowei* Walcott, 1905; *Lingulepis spatula* Walcott, 1902; *Lingulepis squamosa* Hall, 1865; *Lingulepis starri* Matthew, 1891.

Diagnosis.--See Holmer and Popov, 2000.

Discussion.--*Lingulepis* is a problematic genus, which, as pointed out by Krause and Rowell 1975, has been employed for especially elongate forms of smooth shelled obolids that would otherwise have been referred to *Lingulella*. Indeed, Walcott (1912) regarded *Lingulepis* as a subgenus of *Lingulella*, noting that the only significant difference between the two is the marked attenuation in the ventral beak of the former. In light of the revised diagnosis of *Lingulella* (Sutton et al., 2000), it is clear that *Lingulepis* is a separate genus, but the genotype needs to be thoroughly reexamined and described to define its diagnostic characters, which are not well understood. Walcott's (1912) illustrations of *Lingulepis acuminata* (pl. 34, figs. 3, 3a-c; pl. 40, figs. 1, 1a-s; pl. 41, figs. 1, 1a-m; pl. 42, figs. 1, 1a-o) may represent up to eight different species, not including the two subspecies, *L. acuminata sequens* and *L. acuminata meeki*, which were also illustrated.

LINGULEPIS cf. ACUMINATA Conrad, 1839

Plate 17, figures 5-11

Lingula acuminata CONRAD, 1839, p. 64; HALL, 1847, p. 9; EMMONS, 1855, p. 203, pl. 4, fig. 9; BILLINGS, 1863, p. 102, figs. 8a-g; CHAPMAN, 1863, p. 187; CHAPMAN, 1864, p. 159, fig. 155.

Lingula antiqua EMMONS, 1842, p. 268, fig. 68; HALL, 1847, p. 9; HALL, 1851, p. 204, pl. 23, figs. 2a-c; OWEN, 1851, p. 170; BILLINGS, 1856, p. 34, fig. 2; HALL, 1862, p. 21, fig. 2; HAYDEN, 1862, p. 73, figs. 1a-b; EMMONS, 1863, p. 92, fig. 77; JAMES, 1895, p. 884, fig. 1.

Lingula prima OWEN, 1851, p. 170; BILLINGS, 1856, p. 34, fig. 1; GRABAU AND SHIMER, 1907, p. 193.

Lingula antiquata EMMONS, 1885, p. 202, pl. 4, fig. 7.

Lingula pinnaformis OWEN, 1852, p. 583, pl. 1b, figs. 4, 6, 8; HALL, 1862, p. 21, fig. 2; HALL, 1863, p. 129, pl. 6, figs. 14-16.

Lingulepis minima WHITFIELD, 1884, p. 141, pl. 14, figs. 1-2; DWIGHT, 1886, p. 208.

Lingulepis pinnaformis (Owen, 1852) MEEK AND HAYDEN, 1865, p. 2, pl. 1, figs. 1a-b; HALL, 1867, p. 107, pl. 1, figs. 14-16, WHITFIELD, 1880, p. 335, pl. 2, figs. 1-4; WHITFIELD, 1882, p. 169, pl. 1, figs. 2-3; DWIGHT, 1886, p. 208; HALL AND CLARKE, 1892a, p. 232, figs. 237-238, pl. 1, figs 16-17; HALL AND CLARKE, 1892b, p. 548, figs. 237-238; HALL AND CLARKE, 1892c, p. 60, figs. 22-23, pl. 1, figs. 35-36; SCHUCHERT, 1897, p. 260; GRABAU AND SHIMER, 1907, p. 193.

Lingulepis dakotensis MEEK AND HAYDEN, 1865, p. 3; WHITFIELD, 1880, p. 337, pl. 2, figs. 10-11.

Lingulepis acuminata (Conrad, 1839) DWIGHT, 1886, p. 208; MATTHEW, 1895, p. 257, pl. 2, figs. 5a-b; SCHUCHERT, 1897, p. 259; WALCOTT, 1897, p. 404; WALCOTT, 1912, p. 545, pl. 34, figs. 3, 3a-c, pl. 40, figs. 1, 1a-s, pl. 41, figs. 1, 1a-m, pl. 42, figs. 1, 1a-o; ULRICH AND COOPER, 1938, p.54.

Obolus (Lingulepis) acuminatus (Conrad, 1839) WALCOTT, 1899, p. 443.

Diagnosis.--Shell thin, elongate oval, one-and-one-half to two times longer than wide. Ventral beak elongate, sharply acuminate, with straight margins. Pseudointerarea with well-developed flexure lines and narrow pedicle groove. Dorsal valve nearly elliptical in outline, with bluntly rounded beak. Pseudointerarea short, crescent shaped, lacking propareas.

Description.--Shell thin; elongate oval; external ornament of concentric growth lines. Ventral valve one-and-a-half to two times longer than wide; average length to width ratio of 1.8; maximum width anterior of midline. Beak elongate, sharply acuminate; margins straight. Pseudointerarea apsacline with median pedicle groove. Propareas long, raised slightly above valve floor; flexure lines well developed. Visceral area not thickened, not pitted. Muscle scars and mantle canals not apparent.

Dorsal valve longer than wide; average length to width ratio of 1.7; maximum width at midline. Beak bluntly rounded; outline nearly elliptical. Pseudointerarea short, crescent shaped; strongly anacline; barely raised above valve floor; lacking propareas. Visceral area slightly thickened, not pitted. Muscle scars and mantle canals not apparent.

Material examined.--Fifty-seven ventral and thirteen dorsal valves from locality A and B, Black Hills, South Dakota.

Occurrence.--Middle Cambrian to Ordovician of the United States and Canada.

Discussion.--The specimens described here are undoubtedly synonymous with those referred to *Lingulepis acuminata*, specifically those specimens illustrated by Walcott (1912) in pl. 40, figs. 1, 1a, 1m, 1p; and pl. 42, figs. 1i, 1k, 1m, 1n. We regard them provisionally as *L. acuminata* because the species is not well defined, and is in need of detailed reexamination in a manner similar to that undertaken by Sutton et al. (2000) with *Lingulella davisii*. The synonymy presented herein includes all reports of the species but no attempt has been made to evaluate their validity.

Lingulepis cf. *acuminata* is distinguished from other species and, indeed, from some other morphologically distinctive specimens previously assigned to *L. acuminata*, by the straight posterolateral margins of the ventral valve, large length to width ratio, and lack of internal features. The length-to-width ratio appears to be the most distinctive characteristic, and varies from 1.4 in the smallest specimens (less than 1 mm in length) to 2.1 in the largest specimens (up to 3 mm in length), and there appears to be a positive correlation between length-to-width ratio and shell size. The majority of specimens examined are between 1 to 2 mm long, and the length to width ratio in this size range is consistently 1.7 to 1.8.

LINGULEPIS cf. ACUMINATA?

Plate 16, figures 12-16

Description.--Shell thin, elongate oval with external ornament of concentric growth lines. Beak elongate, sharply acuminate. Posterolateral margins initially straight, but flare ventrally creating convex arches on anterior half of margins. Pseudointerarea apsacline with median pedicle groove. Propareas long, slightly above valve floor; flexure lines well developed. Visceral area not thickened, not pitted. Muscle scars and mantle canals not apparent.

Material examined.--One ventral valve from locality B, Black Hills, South Dakota.

Occurrence.--Lower Upper Cambrian (Marjuman Stage), South Dakota.

Discussion.--The arches on the posterolateral valve margins are unlike any structure previously described in an obolid. The fact that only one valve has been found with these arches and that it is, in all other respects, identical to *Lingulepis* cf. *acuminata* described above, suggests that this is a unique morphological anomaly and could have been caused by a random mutation.

Family HOLMERELLIDAE new family

Diagnosis.--Shell dorsibiconvex, subcircular to elongate; larval shell with pitted microornamentation; postlarval shell smooth. Pseudointerareas vestigial or absent.

Occurrence.--Lower Upper Cambrian (Marjuman Stage) of South Dakota.

Included genera.--*Holmerellus* n. gen.

Discussion.--The combination of a pitted larval shell, smooth postlarval shell, and virtually nonexistent pseudointerarea makes the Holmerellidae unique among the Linguloidea. Pitted microornamentation usually occurs either in both the larval and postlarval shells, as in the Zhanatellidae, Elkaniidae, Paterulidae, and Dysoristidae, or is absent altogether, as in the Obolidae and Lingulellotretidae. The only family in which the larval shell is pitted and the postlarval shell is not is the Eoobolidae, which has a pustulose postlarval shell. Indeed, it is the Eoobolidae with which the holmerellids seem most closely related, and *Holmerellus convexus* n. sp. is similar to *Eoobolus* Matthew, 1902 in many respects.

Genus HOLMERELLUS new genus

Type Species.--*Holmerellus convexus* n. sp.

Included species.--*Holmerellus convexus* n. sp., *Holmerellus acuminatus* n. sp., *Holmerellus limbatus* n. sp.

Diagnosis.--Shell dorsibiconvex, subcircular to elongate. Larval shell pitted; post-larval shell ornamented with fine, concentric growth lines; endopunctate. Ventral pseudointerarea vestigial or absent; pedicle groove well defined; pedicle sinus extending one-half valve length. Dorsal valve with vestigial, undivided pseudointerarea. Larval shell sulcate. Two elongate, sub-parallel callosities extend posteriorly from pseudointerarea to two-thirds of valve length, terminating at anterior adductor muscle scars.

Etymology.--Named for brachiopod paleontologist, Lars E. Holmer.

Occurrence.--Lower Upper Cambrian (Marjuman Stage) of South Dakota.

Discussion.--*Holmerellus* resembles *Eobolus* Matthew, 1902 in its overall shell shape, and in having a deeply incised pedicle groove in the ventral valve, and two subparallel callosities in the dorsal valve. It differs, however, in lacking the finely pustulose post-larval ornamentation, elevated ventral pseudointerarea, and elevated, divided dorsal pseudointerarea, which are diagnostic characters of the Eoobolidae. It shares some features in common with the zhanatellid *Canalilatus* Pelman, 1983, particularly its pseudointerareas, but while *Holmerellus* has a pitted larval shell, it lacks the post-larval pitting characteristic of the Zhanatellidae. Its pitted larval shell and smooth adult shell excludes *Holmerellus* from any known lingulid family.

HOLMERELLUS CONVEXUS new species

Plate 18, figures 1-14

Diagnosis.--Shell strongly dorsibiconvex, elongate in outline. Dorsal valve deeply convex . Dorsal and ventral lateral margins with slight dorsal curvature.

Description.--Shell dorsibiconvex, elongate oval in outline, longer than wide, endopunctate. Exterior glossy, with pitted larval shell and post-larval ornament of fine, concentric growth lines.

Ventral valve lacking pseudointerarea. Pedicle groove deeply incised, continuing anteriorly as pedicle sinus, extending to one-half valve length. Circular posterior adductor muscle scars located near posterolateral margins on either side of pedicle groove in beak. Elongate anterior adductor muscle scars located near lateral margins approximately one-third of valve length from beak. *Vascula lateralia*

diverge anteriorly from beak to one-half of valve length. Limbus broadens anteriorly, tapers out near beak.

Dorsal larval shell sulcate; pseudointerarea absent. Two elongate subparallel callosities extend anteriorly from beak to two-thirds of valve length, terminating at anterior adductor muscle scars. Two posterior adductor muscle scars located near posterolateral margins. Neither *vascula lateralia*, nor *vascula media* apparent Broad limbus narrows posteriorly.

Etymology.--Latin, *convexus*, arched outward, referring to the lateral curvature in the dorsal direction of the valves.

Type.--Holotype, USNM 527192, ventral valve: Deadwood Formation, Black Hills, South Dakota.

Other material examined.--Sixty-nine ventral valves and one hundred and thirty-two dorsal valves from locality B, Black Hills, South Dakota.

Occurrence.--Lower Upper Cambrian (Marjuman Stage) of South Dakota.

Discussion.--*Holmerellus convexus* n. sp. is more deeply convex than the other species of the genus, and has an elongate outline that is readily distinguished from the subcircular outlines of the other species.

HOLMERELLUS ACUMINATUS new species

Plate 19, figures 1-14

Diagnosis.--Shell dorsibiconvex, subcircular in outline. Ventral apex acuminate, bisected by emarginature. Pseudointerarea vestigial, strongly anacline,

barely raised above valve floor. Dorsal pseudointerarea vestigial, strongly apsacline, barely raised above valve floor.

Description.--Shell dorsibiconvex, subcircular in outline, as wide as long; endopunctate. External surface glossy, with pitted larval shell and post-larval ornament of fine, concentric growth lines.

Ventral pseudointerarea vestigial, strongly anacline, barely raised above valve floor. Well defined pedicle groove, with pedicle sinus extending to one-half valve length. Posterior margins taper to sharp point at apex, bisected by semicircular emarginature at tip. Vascula lateralia not apparent.

Dorsal larval shell sulcate. Pseudointerarea vestigial, short, strongly apsacline, barely raised above valve floor. Two elongate subparallel callosities extend anteriorly from beak to two-thirds of valve length, terminating at anterior adductor muscle scars. Neither *vascula lateralia*, nor *vascula media* apparent.

Etymology.--Latin, *acuminatus*, pointed, sharpened, referring to sharply pointed ventral apex.

Types.--Holotype, USNM 527196, ventral valve: Deadwood Formation, Black Hills, South Dakota.

Other material examined.--Seventy-four ventral valves and one hundred and two dorsal valves from locality B, Black Hills, South Dakota.

Occurrence.--Lower Upper Cambrian (Marjuman Stage) of South Dakota.

Discussion.--*Holmerellus acuminatus* n. sp. is most readily distinguished from the other species by its sharply acuminate apex. It differs also from *Holmerellus convexus* n. sp. in its subcircular outline, and from *H. limbatus* n. sp. in

lacking a limbus. Neither *vascula lateralia*, nor posterolateral scars are apparent in any specimens of *Holmerellus acuminatus*, but are well defined in both *H. convexus* and *H. limbatus*.

HOLMERELLUS LIMBATUS new species

Plate 20, figures 1-12

Diagnosis.--Shell dorsibiconvex, subcircular in outline. Ventral umbo forms obtuse angle. Ventral pseudointerarea vestigial, strongly anacline, barely raised above valve floor. Dorsal pseudointerarea vestigial, apsacline. Ventral and dorsal valves with broad limbus.

Description.--Shell dorsibiconvex, subcircular in outline, as wide as long; endopunctate. External surface glossy, with pitted larval shell and post-larval ornament of fine, concentric growth lines.

Ventral umbo forms obtuse angle with rounded beak. Pseudointerarea vestigial, strongly apsacline, barely raised above valve floor. Pedicle groove continues anteriorly as pedicle sinus extending to one-half valve length. *Vascula lateralia* extend from posterolateral muscle scars to one-half valve length. Broad limbus surrounds anterior two-thirds of valve margin.

Dorsal larval shell sulcate. Pseudointerarea vestigial, apsacline, with shallow median depression. Broad limbus surrounds margin, tapering in posterior one-third of valve.

Etymology.--Latin, *limbatus*, bordered, referring to distinctive limbus surrounding valve margins.

Types.--Holotype, USNM 527201, ventral valve: Deadwood Formation, Black Hills, South Dakota.

Other material examined.--Ten ventral and seven dorsal valves from locality B, Black Hills, South Dakota.

Occurrence.--Lower Upper Cambrian (Marjuman Stage) of South Dakota.

Discussion.--*Holmerellus limbatus* n. sp. is similar to *H. acuminatus* n. sp. in its shell shape and pseudointerareas, but differs in the obtuse angle of its umbo, which is readily distinguishable from the acutely tapered umbo of *H. acuminatus*, and by the broad limbus that surrounds the margins of both the ventral and dorsal valves.

Family ZHANATELLIDAE Koneva, 1986

Genus DIANABELLA new genus

Type species.--*Dianabella artemisia* new species.

Diagnosis.--Shell elongate oval with bluntly rounded apex. External ornament of obliquely angled punctae in both the larval and postlarval shells. Pseudointerarea broad, anacline with prominent growth lines, divided by shallow, triangular pedicle groove. Pseudointerarea apsacline, broad, undivided, with prominent growth lines and flexure lines. Visceral area diamond-shaped, coarsely pitted. Posterolateral muscle scars small, oval. Central muscle scars minute, circular.

Etymology.--After the primary author's wife, Diana.

Occurrence.--Upper Cambrian of South Dakota.

Discussion.--*Dianabella* is most readily distinguished from other zhanatellids by its elongate oval shell shape, large, broad pseudinterareas with prominent growth lines, and diamond-shaped visceral area in the dorsal valve.

DIANABELLA ARTEMISIA new species

Plate 21, figures 5-16

Diagnosis.--Same as for genus.

Description.--Shell elongate oval, approximately one and one-half times longer than wide. External ornament of obliquely angled punctae oriented towards the right side of each valve.

Ventral valve with bluntly rounded apex. Pseudointerarea large, broad, ornamented with prominent growth lines, divided by shallow triangular pedicle groove. Propareas anacline, raised slightly above valve floor; flexure lines well developed. Muscle scars not apparent. *Vascula lateralia* shallow, short, extending only a short distance beyond pseudointerarea.

Dorsal valve with bluntly rounded apex, only slightly narrower than anterior base. Pseudointerarea large, broad, crescent-shaped, undivided, apsacline, only barely raised above valve floor, ornamented with prominent growth lines; flexure lines located near posterolateral margins. Visceral area diamond-shaped, coarsely pitted. *Vascula lateralia* located near lateral margins, extending to nearly one-half of valve length. *Vascula media* deeply impressed, diverging anteriorly from midpoint of valve. Posterolateral muscle scars small, oval. Central muscle scars minute, circular, narrowly separated, just posterior of midpoint of valve.

Etymology.--Named for Artemis, Greek goddess of wilderness, the hunt, and wild animals.

Types.--Holotype, USNM 527207, dorsal valve: Deadwood Formation, Black Hills, South Dakota.

Other material examined.--Three ventral valves and ten dorsal valves from locality B, Black Hills, South Dakota.

Occurrence.--Lower Upper Cambrian (Marjuman Stage) of South Dakota.

Discussion.--There are many distinctive features that make *Dianabella artemisia* readily distinguishable. Its bluntly oval shell shape, with the apex nearly as wide as the base, is instantly recognizable as are the prominent growth lines on the pseudointerareas. The dorsal valve is especially distinctive with its pitted, diamond-shaped visceral area, deeply impressed *vascula media*, and very small muscle scars.

Genus GANOTOGLOSSA new genus

Type species.--*Ganotoglossa leptotropis*.

Diagnosis.--Shell relatively large, biconvex, with glossy exterior. Larval shell minute. Ventral valve elongate subcircular. Posterior margins straight, forming apical angle of approximately ninety to one-hundred degrees. Pseudointerarea anacline, divided by deep, narrow pedicle groove; propareas raised above valve floor. Shallow pedicle sinus extends anteriorly from pedicle groove to nearly one-half valve length. Dorsal valve subcircular. Pseudointerarea vestigial,

undivided. Two subparallel callosities extend posteriorly from beak to one-half valve length, terminating at thickened central muscle scars.

Etymology.--Greek, *ganotos*, polished; *glossa*, tongue.

Occurrence.--Upper Cambrian of South Dakota.

Discussion.--*Ganotoglossa* is similar to the zhanatellid *Tropidoglossa* Rowell, 1966. It has a similar ventral pseudointerarea and, like *Tropidoglossa* has a ventral larval keel and dorsal larval ridges, although much smaller and less conspicuous than those of *Tropidoglossa*. It differs significantly in overall shell shape and size and, most especially, in the features of the dorsal interior, including its thickened central muscle scars and elongate callosities, well-defined posterolateral muscle scars, and mantle canals, whereas the dorsal valve interiors of *Tropidoglossa* are essentially featureless.

Ganotoglossa is more similar to *Holmerellus* n. gen, particularly with respect to the valve interiors, differing significantly only in having a pitted postlarval shell.

GANOTOGLOSSA LEPTOTROPIS new species

Plate 22, figures 1-14

Diagnosis.--As for genus.

Description.--Shell relatively large, equibiconvex with glossy exterior. Ornament of fine concentric growth lines, and faint radial costae in umbonal region. Larval and postlarval shell pitted. Valve floors endopunctate.

Ventral valve elongate subcircular with straight posterior margins forming obtuse apical angle between ninety and one-hundred degrees. Larval shell minute, with very small, indistinct keel on ventral surface. Pseudointerarea anacline with deep, narrow pedicle groove; propareas broad, triangular, raised above valve floor. Pedicle sinus extends anteriorly from pedicle groove to nearly one-half valve length. Posterolateral muscle scars small, elongate. Central muscle scars relatively large, transversely oval. *Vascula lateralia* baculate, arcuate, extending anteriorly from pseudointerarea to past midlength of valve, tangential to inside edge of posterolateral muscle scars and outside edge of central muscle scars.

Dorsal valve subcircular. Larval shell minute with very shallow depression on dorsal surface. Pseudointerarea vestigial, undivided. Posterolateral muscle scars small, elongate. Central muscle scars small elongate, thickened, raised slightly above valve floor. Two elongate subparallel callosities extend from beak to central muscle scars. *Vascula lateralia* baculate, impressed high on lateral valve walls, tangential to inside edge of posterolateral muscle scars.

Etymology.--Greek, *leptos*, fine, small; *tropis*, keel.

Types.--Holotype, USNM 527211, ventral valve: Deadwood Formation, Black Hills, South Dakota.

Other material examined.--Twenty-two ventral valves and twenty-eight dorsal valves from locality 'B,' Black Hills, South Dakota.

Occurrence.--Lower Upper Cambrian (Marjuman Stage) of South Dakota.

Discussion.--*Ganotoglossa leptotropis* n. sp. is readily identifiable by the glossy lustre of its shell exteriors and its unusually small larval shells bearing the

tiny, ventral keel and dorsal sulcus. It is similar to *Holmerellus acuminatus* n. sp. in shell shape and internal features. It differs primarily in its glossy shell, minute larval shell, and having a pitted postlarval shell.

Genus WAHWAHLINGULA Popov, Holmer, and Miller, 2002

Type species.--*Lingula antiquissima* Jeremejew, 1856.

Diagnosis.--See Popov et al. (2002).

Occurrence.--Upper Cambrian of northwestern Russia, Utah, and South Dakota.

Discussion.--As noted by Popov et al. (2002), *Wahwahlingula* is distinguished from *Lingulella* only by its microornamentation of pitting in the larval and postlarval exteriors, as opposed to the smooth external shell of *Lingulella*. The internal characteristics of *Wahwahlingula* correspond in all respects with *Lingulella* as revised by Sutton et al. (2000). The diagnostic pitting in *Wahwahlingula* is minute and nearly impossible to see without scanning electron microscopy. It is, therefore, very easy to mistake *Wahwahlingula* for *Lingulella*.

WAHWAHLINGULA sp.

Plate 21, figures 1-4

?*Wahwahlingula* sp. POPOV, HOLMER, AND MILLER, 2002, p. 221, fig. 4.17-4.27.

Description.--Dorsal valve ovate with rounded apex. Pseudointerarea short, anacline, barely raised above valve floor, with shallow median depression.

Propareas short, flexure lines weakly developed, located near lateral margins. Valve floor pitted. Microornamentation of fine punctae, penetrating shell at oblique angle to shell surface, directed toward left side of valve.

Material examined.--One dorsal valve from locality 'B,' Black Hills, South Dakota.

Occurrence.--Lower Upper Cambrian (Marjuman Stage) of South Dakota; possibly upper Upper Cambrian (Sunwaptan Stage) to ?Lower Ordovician of Utah.

Discussion.--This specimen of *Wahwahlingula* is nearly identical to *Wahwahlingula* sp. described by Popov et al. (2002), differing only in the nature of the microornamentation. The specimen described here has regularly shaped, obliquely angled punctae, rather than the irregularly shaped, subcircular pits illustrated by Popov et al. (2002, figs. 4.19, 4.25).

Genus TROPIDOGLOSSA Rowell, 1966

Type species.--*Linnarssonella modesta* Walcott, 1908.

Diagnosis.--Shell small, thin, dorsibiconvex; elongate oval to subtriangular in outline. Larval and postlarval shell with pitted microornamentation. Ventral beak with prominent elongated keel; dorsal beak with two short ridges diverging anteriorly. Ventral pseudointerarea orthocline to anacline with deep pedicle groove and well-developed flexure lines; dorsal pseudointerarea narrow with median depression.

Discussion.--The addition of *Tropidoglossa costata* n.sp. to what was previously a monospecific genus expands the understanding of the group but

demands only minimal modification to the diagnosis. The type species was described as having an orthocline ventral pseudointerarea, whereas the ventral pseudointerarea in *Tropidoglossa costata* shows pseudointerareas that are anacline, often barely raised above the valve floor. The prominent ventral keel and subparallel dorsal larval ridges are the critical diagnostic characters that distinguish *Tropidoglossa* from other zhanatellids.

TROPIDOGLOSSA COSTATA new species

Plate 23, figures 1-16

Diagnosis.--Valves costate, with well-defined larval shells. Ventral pseudointerarea anacline, divided by pedicle groove. Dorsal pseudointerarea short, apsacline, with median depression.

Description.--Shell small, thin, dorsibiconvex, subcircular to subtriangular in outline. Valves costate, with pitting in both larval and postlarval shells.

Ventral valve subtriangular with elongated keel on well-defined larval shell. Pseudointerarea anacline, divided by pedicle groove. Shallow *vascula lateralia* diverge anteriorly from pseudointerarea to one third of valve length.

Dorsal valve subcircular, with two subparallel ridges bounding a depression on well-defined larval shell. Pseudointerarea short, apsacline, with median depression. Small anterior adductor scars located centrally on either side of low, short median ridge.

Etymology.--Latin, *costatus*, ribbed.

Types.--Holotype, USNM 527217, ventral valve: Deadwood Formation, Black Hills, South Dakota.

Other material examined.--Eighty-six ventral valves, ninety-four dorsal valves, and three conjoined shells from localities A, and B, Black Hills, South Dakota.

Occurrence.--Lower Upper Cambrian (Marjuman Stage) of South Dakota.

Discussion.--*Tropidoglossa costata* n. sp. is most readily distinguished from the type species by its costate ornamentation, and its anacline ventral pseudointerarea.

VANGAPOROSA new genus

Type species.--*Vangaporosa dakotaensis* n. sp.

Diagnosis.--Shell subrectangular in outline with microornamentation of fine punctae, penetrating larval and postlarval shell at oblique angle to shell surface, directed toward midline of valve. Central region of valve exteriors flat to slightly sulcate, expanding anteriorly from umbo. Ventral pseudointerarea anacline with triangular intertrough. Dorsal pseudointerarea catacline, undivided.

Etymology.--Latin, *vanga*, spade; *porosus*, full of holes.

Occurrence.--Upper Cambrian of South Dakota.

Discussion.--*Vangaporosa* is most readily distinguished by its subrectangular outline and flattened or slightly sulcate central region. The obliquely angled punctae, which give the shell a dull, matte appearance under low

magnification, are similar to those of *Dianabella* and *Wahwahlingula* sp. described above. The valve interiors have few distinguishing characteristics.

VANGAPOROSA DAKOTAENSIS new species

Plate 26, figures 1-11

Diagnosis.--As for genus

Description.--Shell subrectangular in outline. External ornamentation of punctae in larval and postlarval shells. Punctae penetrate shell at an oblique angle, with punctal opening directed away from margins, toward midline of valve. Central region of valve exteriors flattened or slightly sulcate; margins of region form obtuse angle with lateral sides of valve.

Ventral pseudointerarea apsacline, with shallow triangular intertrough, propareas vestigial. Shallow pedicle trough extends anteriorly from beak to one-third of valve length, with low ridge bisecting trough longitudinally. Mantle canals and muscle scars not apparent.

Dorsal pseudointerarea broad, catacline, undivided. Mantle canals and muscle scars not apparent.

Etymology.--*dakotaensis*, for the state of South Dakota.

Types.--Holotype, USNM 527231, dorsal valve: Deadwood Formation, Black Hills, South Dakota.

Other material examined.--Fourteen ventral valves and fourteen dorsal valves from localities A, and B, Black Hills, South Dakota.

Occurrence.--Lower Upper Cambrian (Marjuman Stage) of South Dakota.

Discussion.--*Vangaporosa dakotaensis* n. sp. is similar to *Dianabella artemesia* n. sp. in its punctae and and also has similar pseudointerareas, but differs in being much smaller, and in having a subrectangular outline with straight posterolateral margins rather than an oval outline.

ZHANATELLIDAE gen. et sp. indet. 1

Plate 27, figures 1-6

Material examined.--Two dorsal valves from locality 'B,' Black Hills, South Dakota.

Occurrence.--Lower Upper Cambrian (Marjuman Stage) of South Dakota.

Discussion.--These zhanatellids, known from only two poorly preserved specimens are similar to the dorsal valves of *Vangaporosa dakotaensis* n. sp. The postlarval shell is ornamented with obliquely angled punctae similar to *Vangaporossa dakotaensis* n. sp., *Dianabella artemisia* n. sp., and *Wahwahlingula* sp., but its larval shell is ornamented by small, circular pits. The transition between the two types of pits is fairly abrupt (Plate 27, figs. 5, 6).

ZHANATELLIDAE gen. et sp. indet. 2

Plate 27, figures 7-13

Material examined.--Four dorsal valves from localities A, and B, Black Hills, South Dakota.

Occurrence.--Lower Upper Cambrian (Marjuman Stage) of South Dakota.

Discussion.--These zhanatellids have an external ornament of large circular pits surrounded by smaller pits (plate 27, fig. 10). These pits are easily seen under low power magnification.

Class PATERINATA Williams et al., 1996

Order PATERINIDA Rowell, 1965

Family PATERINIDAE Schuchert, 1893

Genus DICTYONITES Cooper, 1956

Type species.--*Dictyonina perforata* Palmer, 1954.

Other species.--*Dictyonites fredriki* Holmer, 1989.

Diagnosis.--See Laurie (2000).

Occurrence.--Upper Cambrian of Arizona, Montana, South Dakota, Tennessee, Texas, and Wyoming; Middle Ordovician of Alabama, Ireland, and Sweden; Upper Ordovician of Kazakhstan and Nevada.

Discussion.--*Dictyonites* is commonly regarded as an exclusively Ordovician genus (e.g. Laurie, 2000), overlooking the fact that Palmer (1954) first described the type species from the Upper Cambrian Riley Formation of Texas and reported its occurrence in the Middle to Upper Cambrian Abrigo limestone of Arizona, the Upper Cambrian to Lower Ordovician Gallatin Formation of Wyoming, the Upper Cambrian Pilgrim Limestone of Montana, and the Upper Cambrian Nolichucky Shale of Tennessee. Cooper (1956) remarked that it was unusual to find such a distinctively Cambrian element as *Dictyonites* in the Middle Ordovician Pratt Ferry

Formation. Its presence in the Deadwood Formation of South Dakota further confirms *Dictyonites* wide stratigraphic range.

DICTYONITES PERFORATA Palmer, 1954

Plate 24, figures 10-18

Dictyonina perforata PALMER, 1954, p. 766, pl. 89, figs. 11, 14.

Dictyonites perforata (Palmer, 1954) COOPER, 1956, p. 188, pl. 9D, figs. 11-13, pl. 10A, figs. 1-10.

?*Dictyonites perforata* (Palmer, 1954) POPOV *in* Nazarov and Popov, 1980, p. 119, pl. 32, figs. 5-9.

Diagnosis.--Ventral valve with high conical profile, dorsal valve with low, almost flat, profile. Pores relatively large.

Description.--Dorsal valve low, with nearly flat profile. Larval shell pustulose. Postlarval shell perforate, producing lace-like appearance in shell; pores increasing in size anteriorly. Pseudinterarea lacking; muscle scars lacking. Valve interior granulose in both larval and postlarval shell (Pl. 24, figs. 17, 18).

Material examined.--Four dorsal valves from locality A, Black Hills of South Dakota.

Occurrence.-- Upper Cambrian of Arizona, Montana, South Dakota, Tennessee, Texas, and Wyoming; Middle Ordovician of Alabama; ?Middle Ordovician of Kazakhstan.

Discussion.--Although these specimens accord, in all respects, with the published descriptions of the type species, they also possess a pustulose larval shell

and a granulose shell composition, which have never been described in previous specimens. *Dictyonites fredriki* does not have a pustulose larval shell, so this feature is clearly not universal in the genus. This does not necessarily mean that these features are not present in the type material of *Dictyonites perforata*, but rather that the type specimens have not been examined at high enough magnification to detect them. The specimens described here are, therefore, assigned with some small reservation to *Dictyonites perforata*.

Genus MICROMITRA Meek, 1873

Iphidea BILLINGS, 1872, p. 477.

Type species.--*Iphidea*? *sculptilis* Meek, 1873.

Diagnosis.--See Laurie (2000).

Occurrence.--Lower to Upper Cambrian

Discussion.--Meek, 1873 proposed *Micromitra* as a possible name for a new species he named *Iphidea*? *sculptilis*, in the event that these specimens should prove to belong to a new genus. The name *Micromitra* was ultimately adopted when it was noted that the name *Iphidea* was already in use for a genus of beetle.

MICROMITRA MODESTA Lochman, 1940

Plate 24, figures 1-9; Plate 25, figures 1-16

Paterina modesta LOCHMAN, 1940, p. 14, pl. 1, figs. 20, 21.

Micromitra modesta (Lochman, 1940) BELL *in* Lochman and Duncan, 1944, p. 144, pl. 18, figs. 1-8, 18, 19; LOCHMAN AND HU, 1960, p. 820, pl. 95, figs. 37-

40; ROBISON, 1964, p. 56, pl. 92, figs. 1-4; GRANT, 1965, p. 96, pl. 8, figs. 3-4; ROBSON, NOWLAN, AND PRATT, 2003, p. 210, figs. 5.8-5.11.

Micromitra cf. *modesta* HENDERSON AND MACKINNON, 1981, p. 307, figs. 12H-K; ZELL AND ROWELL, 1988, p. 140, figs. 9.6-9.8, 9.10; KONEVA, 1992, p. 98, pl. 11, figs. 10-11; HOLMER, POPOV, KONEVA, AND BASSETT, 2001, p. 29, pl. 42, fig. 10.

Micromitra paucicostellae LOCHMAN, 1940, p. 14, pl. 1, figs. 23, 24.

Diagnosis.--Delthyrium high, notothyrium short. Homeodeltidium and homeochilidium minute. Surface ornamentation of concentric growth fila unbroken by radiating costae.

Description.--Shell ventribiconvex, semicircular in outline, posterior margin straight. Larval shell pustulose; postlarval shell with ornament of concentric growth fila unbroken by radiating costae. Ventral valve high with large delthyrium. Dorsal valve low, nearly flat with small notothyrium. Internal features not apparent.

Material examined.--Twenty-eight ventral valves and twenty-six dorsal valves from locality B, Black Hills, South Dakota.

Occurrence.--Upper Cambrian of Alberta, Missouri, Montana, South Dakota, and Wyoming; possibly Middle Cambrian of Malyi Karatau, North Greenland, and Utah.

Discussion.--Close similarities between species of *Micromitra* and *Paterina* have created difficulities in defining their specific characteristics, which have resulted in many incorrectly identified specimens of these two genera. This situation is exacerbated by the fact that internal features are seldom preserved. Two

of the most distinctive features of *Micromitra modesta* are its minute homeochelidia and homeodeltidia, but they are often not present. The only consistent diagnositic feature of *M. modesta* is the concentric fila on the postlarval shell. Unlike other species of *Micromitra*, these fila are unbifurcated, and unbroken by costae. It may be argued that surface ornament is not a reliable diagnostic characteristic, but it does appear to differ consistently between species, and in many paterinids it is the only diagnostic feature available.

Specimens from western Newfoundland, described by Robson and Pratt (2001) as *Micromitra modesta* are incorrectly identified and are most likely a species of *Paterina*, comparing closely to *Paterina alaica* Imanaliev and Pelman, 1988. These specimens are also similar to those described as *Micromitra* sp. by Holmer, Popov, and Lehnert (2001). Specimens assigned to *Micromitra modesta* by Robison (1964, pl. 92, figs. 1-4), and to *Micromitra* cf. *modesta* by Henderson and MacKinnon (1981, figs. 12H-K), also likely belong to other species.

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EXPLANATION OF PLATES

Geographic and stratigraphic locations of specimens are indicated by locality (A or B), unit, and height in metres above base of unit (e.g. A-1-8 = locality A, unit 1, 8 m above base of unit 1). Refer to figures 2 and 3 for stratigraphic sections.

Plate 1

Figs. 1-9. *Apsotreta orifera* Palmer, 1954.

1. Ventral interior, USNM 527098, A-1-8, x13.
2. Ventral interior, USNM 527098, A-1-8, x11.
3. Ventral interior, lateral oblique view, USNM 527098, A-1-8, x15.
4. Ventral interior, detail of apical process, USNM 527098, A-1-8, x27.
5. Ventral exterior, posterolateral oblique view, USNM 527098, A-1-8, x14.
6. Dorsal interior, USNM 527099, A-1-8, x14.
7. Dorsal interior, lateral view, USNM 527099, A-1-8, x20.
8. Dorsal interior, USNM 527100, A-1-8, x14.
9. Dorsal interior, detail of pseudointerarea, USNM 527100, A-1-8, x24.

Figs. 10-13. *Apsotreta* sp.

10. Ventral interior, USNM 527101, B-4-4, x27.
11. Ventral exterior, detail of larval shell and pedicle foramen, USNM 527102, B-4-4, x267.
12. Ventral exterior, lateral oblique view, USNM 527102, B-4-4, x37.
13. Ventral exterior, USNM 527102, B-4-4, x35.

Plate 2

Figs. 1-13. *Canthylotreta parislata* n. sp.

1. Ventral interior, Holotype, USNM 527103, A-1-8, x14.
2. Ventral interior, Holotype, USNM 527103, A-1-8, x15.
3. Ventral interior, lateral oblique view, Holotype, USNM 527103, A-1-8, x23.
4. Ventral exterior, USNM 527104, A-1-8, x11.
5. Ventral exterior, detail of umbo, USNM 527104, A-1-8, x48.
6. Ventral interior, lateral oblique view, USNM 527105, A-1-8, x14.
7. Ventral exterior, posterior view, USNM 527104, A-1-8, x13.
8. Dorsal interior, detail of pseudointerarea, USNM 527106, A-1-8, x27.
9. Ventral exterior, posterolateral view, USNM 527104, A-1-8, x14.
10. Dorsal interior, USNM 527106, A-1-8, x17.
11. Dorsal interior, USNM 527108, A-1-8, x23.
12. Dorsal exterior, USNM 527107, A-1-8, x22.
13. Dorsal interior, lateral oblique view, USNM 527106, A-1-8, x24.
14. Dorsal exterior, posterior view, USNM 527107, A-1-8, x24.
15. Dorsal exterior, posterolateral view, USNM 527107, A-1-8, x24.
16. Dorsal interior, lateral oblique view, USNM 527106, A-1-8, x34.
17. Dorsal exterior, detail of umbo, USNM 527107, A-1-8, x34.

Plate 3

Figs. 1-6. *Canthylotreta* sp.

1. Ventral interior, USNM 527109, B-5-1, x15.
2. Ventral interior, USNM 527109, B-5-1, x19.
3. Ventral interior lateral oblique view, USNM 527109, B-5-1, x25.
4. Ventral valve, posterior oblique view, USNM 527109, B-5-1, x14.
5. Ventral valve, lateral view, USNM 527109, B-5-1, x16.
6. Ventral valve, detail of beak, USNM 527109, B-5-1, x57.

Figs. 7-13. *Quadrisonia* sp.

7. Ventral interior, USNM 527121, B-5-1, x17.
8. Ventral interior, USNM 527121, B-5-1, x23.
9. Ventral interior, lateral oblique view, USNM 527121, B-5-1, x24.
10. Ventral exterior, posterolateral view, USNM 527122, B-5-1, x17.
11. Ventral exterior, posterior view, USNM 527122, B-5-1, x27.
12. Ventral exterior, lateral oblique view, USNM 527122, B-5-1, x25.
13. Ventral exterior, detail of larval shell and pedicle foramen, USNM 527122, B-5-1, x58.

Plate 4

Figs. 1-9. *Dactylotreta redunca* Rowell and Henderson, 1978.

1. Ventral interior, USNM 527110, B-4-3, x37.
2. Ventral interior, detail of apical process, USNM 527110, B-4-3, x55.
3. Ventral exterior, lateral view, USNM 527111, B-4-3, x55.
4. Ventral exterior, posterior view, USNM 527111, B-4-3, x49.
5. Ventral exterior, detail of larval shell and pedicle foramen, USNM 527111, B-4-3, x163.
6. Dorsal interior, USNM 527112, B-4-3, x28.
7. Dorsal interior, USNM 527112, B-4-3, x30.
8. Dorsal interior, posterolateral oblique view, USNM 527112, B-4-3, x37.
9. Dorsal interior, lateral oblique view, USNM 527112, B-4-3, x31.

Figs. 10-17. *Physotreta spinosa* Walcott, 1905.

10. Ventral interior, USNM 527113, B-4-4, x21.
11. Ventral exterior, USNM 527114, B-4-4, x45.
12. Ventral exterior, lateral view, USNM 527114, B-4-4, x36.
13. Dorsal interior, posterolateral oblique view, USNM 527115, B-4-4, x25.
14. Dorsal exterior, lateral oblique view, USNM 527116, B-4-4, x44.
15. Dorsal interior, USNM 527115, B-4-4, x23.
16. Dorsal exterior, USNM 527116, B-4-4, x30.
17. Dorsal interior, lateral oblique view, USNM 527115, x27.

Plate 5

Figs. 1-13. *Quadrisonia*? *sigmoidea* n. sp.

1. Ventral exterior, posterolateral oblique view, USNM 527117, B-4-3, x53.
2. Ventral exterior, posterior view, USNM 527117, B-4-3, x60.
3. Ventral exterior, lateral view, USNM 527117, B-4-3, x45.
4. Ventral exterior, detail of larval shell and pedicle foramen, USNM 527117, B-4-3, x163.
5. Ventral interior, Holotype, USNM 527118, B-4-3, x42.
6. Ventral interior, detail of internal foramen, Holotype, USNM 527118, B-4-3, x333.
7. Dorsal interior, USNM 527119, B-4-3, x30.
8. Dorsal interior, USNM 527119, B-4-3, x26.
9. Dorsal interior posterolateral oblique view, USNM 527119, B-4-3, x50.
10. Dorsal interior, lateral view, USNM 527119, x46.
11. Dorsal exterior, USNM 527120, B-4-3, x29.
12. Dorsal exterior, lateral view, USNM 527120, B-4-3, x44.
13. Dorsal exterior, posterolateral oblique view, USNM 527120, B-4-3, x35.

Plate 6

Figs. 1-18. *Amplitreta cyclopis* n. gen. et n. sp.

1. Ventral interior, Holotype, USNM 527123, A-1-8, x22.
2. Ventral interior, Holotype, USNM 527123, A-1-8, x25.
3. Ventral interior, posterior oblique view, Holotype, USNM 527123, A-1-8, x24.
4. Ventral interior, detail of internal foramen, Holotype, USNM 527123, A-1-8, x91.
5. Ventral exterior, lateral oblique view, Holotype, USNM 527123, A-1-8, x41.
6. Ventral exterior, posterior view, Holotype, USNM 527123, A-1-8, x51.
7. Ventral exterior, USNM 527124, A-1-8, x30.
8. Ventral exterior, posterior view, USNM 527124, A-1-8, x38.
9. Ventral exterior, lateral view, USNM 527124, A-1-8, x40.
10. Dorsal interior, USNM 527126, A-1-8, x29.
11. Dorsal interior, lateral view, USNM 527126, A-1-8, x29.
12. Dorsal interior, USNM 527126, A-1-8, x37.
13. Dorsal interior, detail of pseudointerarea, USNM 527125, A-1-8, x40.
14. Dorsal interior, USNM 527125, A-1-8, x24.
15. Dorsal interior, anterolateral oblique view, USNM 527125, A-1-8, x51.
16. Dorsal interior, lateral view, USNM 527125, A-1-8, x28.
17. Dorsal exterior, lateral view, USNM 527127, A-1-8, x30.
18. Dorsal exterior, USNM 527127, A-1-8, x18.

Plate 7

Figs. 1-14. *Amplitreta elongata* n. gen. et n. sp.

1. Ventral exterior, lateral view, Paratype, USNM 527128, B-4-5, x57.
2. Ventral interior, Holotype, USNM 527129, B-4-5, x38.
3. Ventral interior, anterolateral oblique view, Holotype, USNM 527129, B-4-5, x37.
4. Ventral exterior, posterior view, Paratype, USNM 527128, B-4-5, x64.
5. Ventral exterior, posterior view, Holotype, USNM 527129, B-4-5, x59.
6. Ventral exterior, posterior view, Paratype, USNM 527128, B-4-5, x188.
7. Dorsal interior, USNM 527131, B-4-5, x40.
8. Dorsal interior, anterolateral oblique view, USNM 527131, B-4-5, x50.
9. Dorsal interior anterior oblique view, USNM 527131, B-4-5, x50.
10. Dorsal interior, detail of pseudointerarea, USNM 527131, B-4-5, x93.
11. Dorsal exterior, Paratype, USNM 527130, B-4-5, x42.
12. Dorsal exterior, detail of larval shell, Paratype, USNM 527130, B-4-5, x127.
13. Dorsal exterior, lateral view, Paratype, USNM 527130, B-4-5, x58.
14. Dorsal exterior, posterior view, Paratype, USNM 527130, B-4-5, x58.

Plate 8

Figs. 1-5. *Eoscaphelasma* cf. *satpakensis* Koneva, Popov and Ushatinskaya, 1990.

1. Ventral exterior, USNM 527157, B-4-5, x43.
2. Ventral exterior, lateral view, USNM 527157, B-4-5, x67.
3. Ventral exterior, detail of larval shell, USNM 527157, B-4-5, x482.
4. Ventral exterior, posterior view, USNM 527157, B-4-5, x40.
5. Ventral interior, USNM 527158, B-4-5, x47.

Figs. 6-17. aff. *Anabolatreta tora* n. sp.

6. Ventral exterior, lateral view, USNM 527133, A-1-4, x25.
7. Ventral exterior, USNM 527133, A-1-4, x20.
8. Ventral interior, Holotype, USNM 527132, A-1-4, x24.
9. Ventral exterior, detail of pedicle foramen, USNM 527133, A-1-4, x80.
10. Ventral exterior, posterior view, USNM 527133, A-1-4, x20.
11. Ventral interior, Holotype, USNM 527132, A-1-4, x21.
12. Ventral interior, anterolateral oblique view, Holotype, USNM 527132, A-1-4, x20.
13. Ventral valve, posterolateral oblique view, Holotype, USNM 527132, A-1-4, x19.
14. Dorsal interior, anterolateral oblique view, Paratype, USNM 527134, A-1-4, x26.
15. Dorsal interior, lateral oblique view, Paratype, USNM 527134, A-1-4, x24.

16. Dorsal interior, USNM 527134, A-1-4, x23.

17. Dorsal interior, anterior oblique view, USNM 527134, A-1-4, x25.

Plate 9

Figs. 1-13. *Opisthotreta nuda* n. sp.

1. Ventral interior, anterolateral oblique view, Holotype, USNM 527135, B-4-1, x65.
2. Ventral interior, anterior oblique view, Holotype, USNM 527135, B-4-1, x74.
3. Ventral interior, lateral oblique view, Holotype, USNM 527135, B-4-1, x65.
4. Ventral valve, lateral view, Holotype, USNM 527135, B-4-1, x105.
5. Ventral interior, posterior oblique view, Holotype, USNM 527135, B-4-1, x61.
6. Ventral exterior, Paratype, USNM 527136, B-4-1, x81.
7. Ventral exterior, detail of beak, Holotype, USNM 527135, B-4-1, x208.
8. Conjoined shell, lateral view, Paratype, USNM 527136, B-4-1, x125.
9. Conjoined shell, posterior view, USNM 527139, B-4-1, x95.
10. Conjoined shell, posterodorsal oblique view, USNM 527139, B-4-1, x85.
11. Dorsal interior, USNM 527137, B-4-1, x49.
12. Conjoined shell, detail of posterior, USNM 527136, B-4-1, x129.
13. Dorsal exterior, USNM 527138, B-4-1, x68.

Plate 10

Figs. 1-11. *Stilpnotreta magna* Henderson and MacKinnon, 1981.

1. Ventral interior, USNM 527140, A-1, x90.
2. Ventral interior, anterior oblique view, USNM 527140, A-1-1, x100.
3. Ventral interior, anterolateral oblique view, USNM 527140, A-1-1, x105.
4. Ventral exterior, USNM 527141, A-1-1, x85.
5. Ventral exterior, posterior oblique view, USNM 527140, A-1-1, x120.
6. Ventral exterior, posterolateral view, USNM 527141, A-1-1, x100.
7. Dorsal exterior, posterolateral view, USNM 527142, A-1-1, x85.
8. Dorsal interior, USNM 527143, A-1-1, x82.
9. Dorsal exterior, USNM 527143, A-1-1, x82.
10. Dorsal interior, detail of pseudointerarea, USNM 527143, A-1-1, x219.
11. Dorsal interior, anterolateral oblique view, USNM 527143, A-1-1, x96.

Plate 11

Figs. 1-16. *Curticia minuta* Bell, 1944.

1. Ventral interior, USNM 527144, B-5-1, x20.
2. Ventral interior, detail of pseudointerarea, USNM 527144, B-5-1, x42.
3. Ventral interior, lateral oblique view, USNM 527144, B-5-1, x18.
4. Ventral interior, posterolateral oblique view, USNM 527145, B-5-1, x23.
5. Ventral interior, detail of pseudointerarea, USNM 527145, B-5-1, x27.
6. Ventral interior, anterior oblique view, USNM 527145, B-5-1, x24.
7. Dorsal interior, USNM 527147, B-5-1, x20.
8. Ventral interior, anterior oblique view, USNM 527145, B-5-1, x24.
9. Ventral exterior, posterolateral view, USNM 527146, B-5-1, x20.
10. Dorsal interior, USNM 527148, B-5-1, x18.
11. Dorsal interior, posterolateral oblique view, USNM 527147, B-5-1, x20.
12. Dorsal interior, detail of pseudointerarea, USNM 527147, B-5-1, x23.
13. Dorsal interior, anterolateral oblique view, USNM 527148, B-5-1, x20.
14. Dorsal exterior, detail of larval shell, USNM 527149, B-5-1, x75.
15. Dorsal exterior, USNM 527149, B-5-1, x25.
16. Dorsal exterior, posterior view USNM 527149, B-5-1, x34.

Plate 12

Figs. 1-16. *Curticia pustulosa* n. sp.

1. Ventral interior, Holotype, USNM 527150, A-1-4, x23.
2. Ventral interior, detail of pseudointerarea, Holotype, USNM 527150, A-1-4, x40.
3. Ventral interior, anterolateral oblique view, USNM 527152, A-1-4, x40.
4. Ventral interior, anterior oblique view, detail of pseudointerarea, USNM 527150, A-1-4, x40.
5. Ventral exterior, USNM 527151, A-1-4, x26.
6. Ventral exterior, detail of shell surface, USNM 527153, x60.
7. Ventral exterior, posterior view, USNM 527151, A-1-4, x25.
8. Ventral exterior, lateral view, USNM 527151, A-1-4, x20.
9. Ventral exterior, detail of pedicle foramen, USNM 527151, x43.
10. Dorsal interior, USNM 527154, x20.
11. Dorsal interior, detail of pseudointerarea, USNM 527154, x25.
12. Dorsal interior, anterolateral oblique view, USNM 527155, x25.
13. Dorsal interior, anterior oblique view, USNM 527155, x15.
14. Dorsal exterior, detail of larval shell, USNM 527156, x200.
15. Dorsal exterior, detail of shell surface, USNM 527156, x250.

Plate 13

Figs. 1-14. *Kotylotreta nupera* n. sp.

1. Ventral interior, Holotype, USNM 527161, B-5-1, x39.
2. Ventral interior, anterolateral view, Holotype, USNM 527161, B-5-1, x39.
3. Ventral interior, anterolateral oblique view, Holotype, USNM 527161, B-5-1, x39.
4. Ventral exterior, USNM 527162, B-5-1, x21.
5. Ventral exterior, posterior view, USNM 527162, B-5-1, x20.
6. Ventral exterior, lateral view, USNM 527162, B-5-1, x29.
7. Ventral exterior, detail of larval shell and pedicle foramen, USNM 527162, B-5-1, x200.
8. Dorsal interior, USNM 527163, B-5-1, x20.
9. Dorsal interior, lateral oblique view, USNM 527163, B-5-1, x28.
10. Dorsal valve, posterior view, USNM 527163, B-5-1, x20.
11. Dorsal interior, anterolateral oblique view, USNM 527163, B-5-1, x20.
12. Dorsal exterior, USNM 527164, B-5-1, x20.
13. Dorsal exterior, lateral view, USNM 527164, B-5-1, x30.
14. Dorsal exterior, posterior view, USNM 527164, B-5-1, x20.

Figs. 15-17. *Kotylotreta undata* Koneva, 1990.

15. Ventral exterior, USNM 527160, B-4-5, x80.

16. Ventral exterior, posterolateral oblique view, USNM 527160, B-4-5, x97.
17. Ventral interior, USNM 527159, B-4-5, x60.

Plate 14

Figs. 1-7. *Dicellomus politus* Hall, 1871.

1. Ventral interior, USNM 527165, B-4-1, x9.
2. Ventral interior, detail of posterior, USNM 527165, B-4-1, x14.
3. Dorsal interior, USNM 527166, B-4-1, x9.
4. Dorsal exterior, USNM 527167, B-4-1, x10.
5. Dorsal interior, anterolateral oblique view, USNM 527166, B-4-1, x11.
6. Dorsal exterior, posterior oblique view, USNM 527167, B-4-1, x13.
7. Dorsal interior, lateral oblique view, USNM 527166, B-4-1 x10.

Figs. 8-16. *Dicellomus* sp.

8. Ventral interior, USNM 527256, B-4-2, x10.
9. Ventral interior, anterior oblique view, USNM 527256, B-4-2, x12.
10. Ventral interior, detail of posterior, USNM 527256, B-4-2, x18.
11. Ventral exterior, USNM 527257, B-4-2, x9.
12. Dorsal interior, lateral oblique view, USNM 527180, B-4-2, x20.
13. Dorsal interior, USNM 527180, B-4-2, x20.
14. Dorsal interior, anterolateral oblique view, USNM 527180, B-4-2, x20.
15. Dorsal interior, detail of pseudointerarea, USNM 527180, B-4-2, x37.
16. Dorsal exterior, posterolateral oblique view, USNM 527181, B-4-2, x20.

Plate 15

Figs. 1-6. *Dicellomus* aff. *parvus* Walcott, 1905.

1. Dorsal interior, USNM 527178, B-4-1, x32.
2. Dorsal interior, anterior oblique view, USNM 527178, B-4-1, x40.
3. Dorsal interior, anterolateral oblique view, USNM 527178, B-4-1, x40.
4. Dorsal interior, lateral oblique view, USNM 527178, B-4-1, x40.
5. Dorsal exterior, USNM 527179, B-4-1, x26.
6. Dorsal exterior, posterior oblique view, USNM 527179, B-4-1, x30.

Figs. 7-10. *Dicellomus* cf. *amblia* Bell, 1944.

7. Ventral interior, USNM 527168, B-4-1, x11.
8. Ventral interior, detail of valve posterior, USNM 527168, B-4-1, x20.
9. Dorsal interior, USNM 527169, B-4-1, x20.
10. Dorsal interior, detail of pseudointerarea, USNM 527169, B-4-1, x40.

Figs. 11-14. *Dicellomus appalachia* Walcott, 1905.

11. Ventral interior, lateral oblique view, USNM 527170, B-4-1, x9.
12. Ventral interior, USNM 527170, B-4-1, x7.
13. Dorsal interior, USNM 527171, B-4-2, x9.
14. Dorsal interior, lateral oblique view, USNM 527171, B-4-2, x13.

Plate 16

Figs. 1-11. *Dicellomus nanus* Meek and Hayden, 1862.

1. Dorsal interior, USNM 527172, B-4-1, x20.
2. Dorsal interior, detail of posterior, USNM 527172, B-4-1, x42.
3. Dorsal interior, anterior oblique view, USNM 527174, B-4-1, x30.
4. Dorsal interior, detail of shell surface, USNM 527172, B-4-1, x395.
5. Dorsal exterior, USNM 527173, B-4-1, x20.
6. Dorsal exterior, lateral view, USNM 527173, B-4-1, x26.
7. Dorsal exterior, detail of umbo, USNM 527173, B-4-1, x62.
8. Dorsal exterior, posterior view, USNM 527173, B-4-1, x28.
9. Ventral interior, USNM 527176, B-4-1, x20.
10. Dorsal interior, lateral oblique view, USNM 527175, B-4-2, x22.
11. Ventral interior, detail of valve posterior, USNM 527176, B-4-1, x40.

Figs. 12-14. *Lingulepis* cf. *acuminata*?

12. Ventral exterior, posterolateral oblique view, USNM 527191, B-4-2, x28.
13. Ventral exterior, posterolateral oblique view, USNM 527191, B-4-2, x36.
14. Ventral exterior, USNM 527191, B-4-2, x35.
15. Ventral exterior, detail of valve posterior, USNM 527191, B-4-2, x41.
16. Ventral exterior, lateral oblique view, USNM 527191, B-4-2, x47.

Plate 17

Figs. 1-4. *Lingulella similis* Walcott, 1898.

1. Ventral interior, USNM 527182, B-4-1, x30.
2. Dorsal interior, USNM 527183, B-4-1, x20.
3. Dorsal exterior, USNM 527184, B-4-1, x22.
4. Dorsal interior, anterolateral oblique view, USNM 527183, B-4-1, x26.

Figs. 5-11. *Lingulepis* cf. *acuminata* Conrad, 1839.

5. Ventral interior, USNM 527185, B-4-2, x30.
6. Ventral interior, USNM 527187, B-4-5, x50.
7. Ventral exterior, USNM 527186, B-4-2, x43.
8. Ventral interior, USNM 527188, B-4-4, x23.
9. Ventral exterior, lateral oblique view, USNM 527186, B-4-2, x38.
10. Dorsal interior, USNM 527189, B-4-4, x30.
11. Dorsal exterior, USNM 527190, B-4-4, x28.

Plate 18

Figs. 1-14. *Holmerellus convexus* n. gen. et n. sp.

1. Ventral interior, Holotype, USNM 527192, B-4-1, x24.
2. Ventral interior, anterior oblique view, Holotype, USNM 527192, B-4-1, x28.
3. Ventral interior, lateral oblique view, Holotype, USNM 527192, B-4-1, x34.
4. Ventral exterior, lateral view, Holotype, USNM 527192, B-4-1, x40.
5. Ventral exterior, USNM 527193, B-4-1, x25.
6. Ventral exterior, detail of larval shell, USNM 527193, B-4-1, x259.
7. Ventral interior, detail of pseudointerarea, USNM 527192, B-4-1, x60.
8. Dorsal interior, USNM 527194, B-4-1, x18.
9. Dorsal interior, detail of pseudointerarea, USNM 527194, B-4-1, x43.
10. Dorsal interior, anterolateral oblique view, USNM 527194, B-4-1, x28.
11. Dorsal exterior, posterior oblique view, USNM 527195, B-4-1, x29.
12. Dorsal exterior, USNM 527195, B-4-1, x20.
13. Dorsal exterior, detail of larval shell, USNM 527195, B-4-1, x143.
14. Dorsal exterior, lateral view, USNM 527195, B-4-1, x23.

Plate 19

Figs. 1-15. *Holmerellus acuminatus* n. gen. et n. sp.

1. Ventral interior, Holotype, USNM 527196, B-4-1, x30.
2. Ventral interior, detail of posterior, Holotype, USNM 527196, B-4-1, x50.
3. Ventral exterior, USNM 527197, B-4-2, x27.
4. Ventral exterior, lateral view, USNM 527197, B-4-2, x36.
5. Ventral exterior, lateral view, detail of larval shell, USNM 527197, B-4-2, x127.
6. Ventral exterior, detail of larval shell, USNM 527197, B-4-2, x166.
7. Dorsal interior, USNM 527199, B-4-1, x30.
8. Dorsal interior, anterior oblique view, USNM 527199, B-4-1, x33.
9. Ventral exterior, posterior view, detail of larval shell, USNM 527198, B-4-1, x100.
10. Dorsal exterior, posterior oblique view, USNM 527200, B-4-1, x34.
11. Ventral interior, detail of shell surface, Holotype, USNM 527196, B-4-1, x230.
12. Dorsal interior, lateral oblique view, USNM 527199, B-4-1, x34.
13. Dorsal interior, detail of pseudointerarea, USNM 527199, B-4-1, x112.
13. Dorsal exterior, detail of larval shell, USNM 537200, B-4-1, x103.

Plate 20

Figs. 1-12. *Holmerellus limbatus* n. gen. et n. sp.

1. Ventral interior, Holotype, USNM 527201, B-4-1, x25.
2. Ventral interior, anterolateral oblique view, Holotype, USNM 527201, B-4-1, x40.
3. Ventral exterior, USNM 527202, B-4-1, x32.
4. Dorsal interior, USNM 527203, B-4-1, x40.
5. Ventral exterior, detail of beak, USNM 527202, B-4-1, x67.
6. Dorsal interior, USNM 527203, B-4-1, x40.
7. Dorsal interior, detail of pseudointerarea, USNM 527203, B-4-1, x107.
8. Dorsal interior, lateral oblique view, USNM 527203, B-4-1, x55.
9. Dorsal exterior, USNM 527204, x38.
10. Dorsal exterior, USNM 527204, posterior view, B-4-1, x48.
11. Dorsal exterior, detail of larval shell, USNM 527204, B-4-1, x136.
12. Dorsal exterior, posterior view, detail of larval shell, USNM 527204, B-4-1, x130.

Plate 21

Figs. 1-4. *Wahwahlingula* sp.

1. Dorsal interior, USNM 527215, B-4-3, x28.
2. Dorsal exterior, USNM 527216, B-4-3, x23.
3. Dorsal exterior, detail of umbo, USNM 527216, B-4-3, x64.
4. Dorsal exterior, lateral oblique view, USNM 527216, B-4-3, x24.

Figures 5-16. *Dianabella artemesia* n. gen. et n. sp.

5. Ventral interior, USNM 527205, B-5-1, x25.
6. Ventral exterior, USNM 527206, B-5-1, x19.
7. Ventral exterior, detail of shell surface, USNM 527206, B-5-1, x213.
8. Ventral interior, anterior oblique view, USNM 527205, B-5-1, 527205, x32.
9. Ventral interior, anterolateral oblique view, USNM 527205, B-5-1, 527205, x30.
10. Dorsal interior, Holotype, USNM 527207, B-5-1, x13.
11. Dorsal interior, Holotype, USNM 527207, B-5-1, x15.
12. Dorsal interior, detail of pseudointerarea, Holotype, USNM 527207, B-5-1, x22.
13. Dorsal interior, anterolateral oblique view, Holotype, USNM 527207, B-5-1, x16.
14. Dorsal exterior, USNM 527208, B-5-1, x18.

15. Dorsal interior, anterior oblique view, Holotype, USNM 527207, B-5-1, x20.
16. Dorsal exterior, detail of shell surface, USNM 527208, B-5-1, x70.

Plate 22

Figs. 1-14. *Ganotoglossa leptotropis* n. gen. et n. sp.

1. Ventral interior, USNM 527209, B-4-5, x22.
2. Ventral interior, anterior oblique view, USNM 527209, B-4-5, x28.
3. Ventral interior, anterolateral oblique view, USNM 527209, B-4-5, x22.
4. Ventral exterior, USNM 527210, B-4-5, x17.
5. Ventral exterior, posterolateral oblique view, USNM 527210, B-4-5, x20.
6. Ventral exterior, posterolateral oblique view, detail of posterior, USNM 527210, B-4-5, x55.
7. Ventral interior, Holotype, USNM 527211, B-4-5, x 20.
8. Dorsal interior, USNM 527213, B-4-5, x20.
9. Ventral exterior, detail of postlarval shell surface, USNM 527212, B-4-5, x955.
10. Ventral exterior, lateral view, USNM 527212, B-4-5, x32.
11. Dorsal interior, anterolateral oblique view, USNM 527213, B-4-5, x26.
12. Dorsal interior, USNM 527213, B-4-5, x20.
13. Dorsal exterior, detail of posterior, USNM 527214, B-4-5, x105.
14. Dorsal interior, detail of pseudointerarea, USNM 527213, B-4-5, x25.

Plate 23

Figs. 1-16. *Tropidoglossa costata* n. sp.

1. Ventral interior, Holotype, USNM 527217, B-4-2, x42.
2. Ventral interior, anterolateral oblique view, Holotype, USNM 527217, B-4-2, x47.
3. Ventral exterior, Holotype, USNM 527217, B-4-2, x55.
4. Ventral exterior, anterolateral oblique view, USNM 527218, B-4-2, x55.
5. Ventral exterior, detail of larval shell, USNM 527219, B-4-3, x85.
6. Ventral exterior, lateral view, detail of larval shell, USNM 527218, B-4-2, x228.
7. Ventral exterior, posterior view, detail of larval shell, USNM 527219, B-4-3, x100.
8. Dorsal interior, USNM 527220, B-4-3, x45.
9. Dorsal interior, anterolateral oblique view, USNM 527220, B-4-3, x45.
10. Dorsal interior, detail of pseudointerarea, USNM 527220, B-4-3, x85.
11. Dorsal exterior, lateral view, USNM 527221, B-4-5, x45.
12. Conjoined shell, posterior view, USNM 527222, B-4-4, x40.
13. Dorsal exterior, USNM 527221, B-4-5, x40.
14. Dorsal exterior, detail of larval shell, USNM 527221, B-4-5, x135.
15. Conjoined shell, lateral view, USNM 527222, B-4-4, x60.
16. Conjoined shell, detail of posterior margin, USNM 527222, B-4-4, x500.

Plate 24

Figs. 1-9. *Micromitra modesta* Lochman, 1940.

1. Dorsal exterior, USNM 527228, B-5-1, x22.
2. Dorsal exterior, detail of larval shell, USNM 527228, B-5-1, x80.
3. Dorsal exterior, lateral view, USNM 527228, B-5-1, x30.
4. Dorsal exterior, posterior view, USNM 527228, B-5-1, x27.
5. Dorsal exterior, posterior view, detail of larval shell, USNM 527228, B-5-1, x47.
6. Dorsal interior, posterior view, USNM 527229, B-5-1, x22.
7. Dorsal interior, USNM 527229, B-5-1, x22.
8. Dorsal interior, anterolateral oblique view, USNM 527229, B-5-1, x22.
9. Dorsal interior, detail of of pseudointerarea, USNM 527229, B-5-1, x55.

Figs. 10-18. *Dictyonites perforata* Palmer, 1954.

10. Dorsal exterior, USNM 527223, A-1-8, x22.
11. Dorsal exterior, posterior view, USNM 527223, A-1-8, x21.
12. Dorsal exterior, detail of larval shell, USNM 527223, A-1-8, x180.
13. Dorsal interior, USNM 527224, A-1-8, x23.
14. Dorsal interior, anterior oblique view, USNM 527224, A-1-8, x20.
15. Dosal exterior, lateral view, USNM 527223, A-1-8, x25.
16. Dorsal interior, detail of pseudointerarea, USNM 527224, A-1-8, x36.
17. Dorsal interior, detail of shell surface at posterior margin, USNM 527224, A-1-8, x155.

18. Dorsal interior, detail of shell surface at anterior margin, USNM 527224, A-1-8, x255.

Plate 25

Figs. 1-16. *Micromitra modesta* Lochman, 1940.

1. Ventral exterior, USNM 527225, B-4-3, x30.
2. Ventral exterior, detail of larval shell, USNM 527225, B-4-3, x57.
3. Ventral exterior, posterior view, USNM 527225, B-4-3, x35.
4. Ventral exterior, lateral view, USNM 527225, B-4-3, x30.
5. Ventral exterior, detail of larval shell, USNM 527225, B-4-3, x260.
6. Ventral exterior, lateral view, detail of larval shell, USNM 527225, B-4-3, x1,630.
7. Ventral exterior, USNM 527226, B-5-1, x25.
8. Ventral exterior, detail of larval shell, USNM 527226, B-5-1, x40.
9. Ventral exterior, posterolateral view, USNM 527226, B-5-1, x25.
10. Ventral interior, USNM 527227, B-5-1, x35.
11. Ventral interior, detail of pseudeointerarea, USNM 527227, B-5-1, x75.
12. Ventral interior, anterior oblique view, USNM 527227, B-5-1, x35.
13. Ventral exterior, posterior view, USNM 527226, B-5-1, x35.
14. Ventral exterior, detail of shell surface, USNM 527226, B-5-1, x370.
15. Ventral exterior, posterior view, USNM 527226, B-5-1, x70.
16. Ventral interior, anterolateral view, USNM 527227, B-5-1, x35.

Plate 26

Figs. 1-11. *Vangaporosa dakotaensis* n. sp.

1. Ventral interior, USNM 527230, B-4-1, x40.
2. Ventral exterior, Holotype, USNM 527231, B-4-1, x30.
3. Ventral exterior, detail of larval shell, Holotype, USNM 527231, B-4-1, x367.
4. Ventral exterior, detail of shell surface, Holotype, USNM 527231, B-4-1, x770.
5. Ventral exterior, USNM 527233, A-1-2, x43.
6. Ventral exterior, detail of larval shell, USNM 527233, A-1-2, x180.
7. Ventral interior, USNM 527232, A-1-2, x15.
8. Ventral interior, detail of pseudointerarea, USNM 527232, A-1-2, x45.
9. Dorsal interior, USNM 527234, B-5-1, x60.
10. Dorsal interior, anterolateral oblique view, USNM 527234, B-5-1, x60.
11. Dorsal exterior, USNM 527235, B-5-1, x50.

Plate 27

Figs. 1-6. Zhanatellidae gen. et sp. indet. 1.

1. Dorsal interior, USNM 527237, B-5-3, x55.
2. Dorsal interior, detail of pseudointerarea, USNM 527237, B-5-3, x85.
3. Dorsal exterior, USNM 527236, B-5-3, x50.
4. Dorsal exterior, detail of postlarval shell surface, USNM 527236, B-5-3, x265.
5. Dorsal exterior, detail of larval margin, USNM 527236, B-5-3, x360.
6. Dorsal exterior, detail of larval shell, USNM 527236, B-5-3, x360.

Figs. 7-13. Zhanatellidae gen. et sp. indet. 2.

7. Dorsal exterior, USNM 527246, B-4-1, x25.
8. Dorsal exterior, USNM 527248, B-4-2, x15.
9. Dorsal exterior, detail of shell surface, USNM 527248, B-4-2, x25.
10. Dorsal exterior, detail of postlarval pitting, USNM 527248, B-4-2, x365.
11. Dorsal exterior, lateral view, USNM 527248, B-4-2, x28.
12. Dorsal exterior, posterior view, USNM 527248, B-4-2, x72.
13. Dorsal exterior, posterior view, USNM 527248, B-4-2, x33.

Fig. 1. Map of study area in the Black Hills of South Dakota. Locality A is a roadcut on highway 385 south of Deadwood. Locality B is an outcrop located next to a logging road at Pole Creek, approximately 15 km southwest of Deadwood.

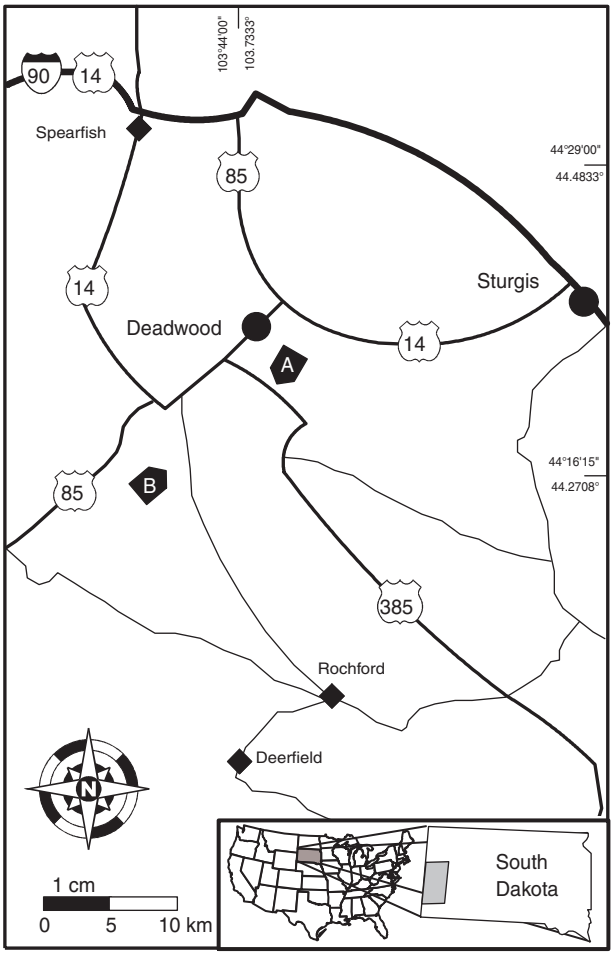
Fig. 2. Stratigraphic distribution of linguliformean brachiopods from locality A, a 9.3 m thick section of flat-pebble limestone conglomerate. Specimens collected at 1 m intervals (1-8).

Fig. 3. Stratigraphic distribution of linguliformean brachiopods from locality B. Unit 1: massive bedded quartz arenite. Unit 2: thin- to medium-bedded medium-grained sandstone interbedded with thin beds of fine-grained glauconitic sandstone. Unit 3: fine-grained sandstone. Unit 4: interbedded shale and flat-pebble limestone conglomerate. Unit 5: interbedded shale and lenticular sandstone. Specimens collected from units 4 and 5 at 1 m intervals (B-4-1 to B-4-5 and B-5-1 to B-5-3).

Fig. 4. Relative abundance of linguliformean genera in four collections from locality A.

Fig. 5. Relative abundance of linguliformean genera in five collection from unit 4 at locality B.

Fig. 6. Relative abundance of linguliformean genera in two collections from unit 5 at locality B.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Spearfish
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Sturgis
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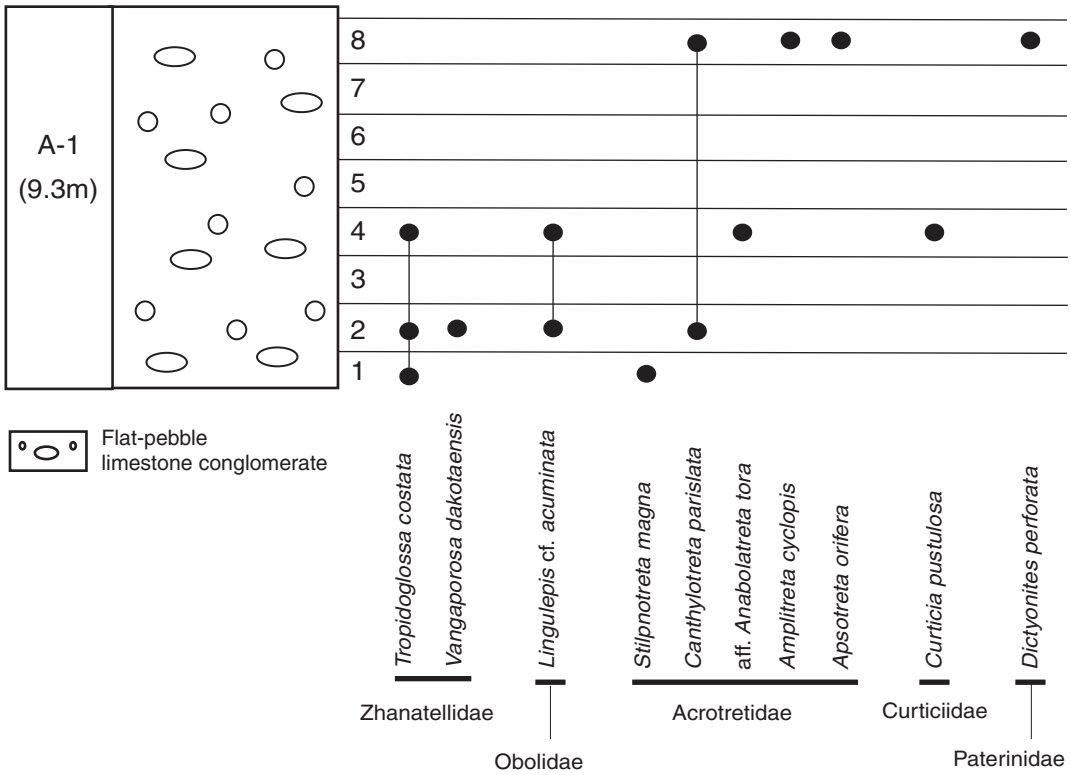
A-1
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Flat-pebble
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Tropidoglossa costata
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Lingulepis cf. acuminata
Stilpnotreta magna
Canthylotreta parislata
aff. Anabolatreta tora
Amplitreta cyclopis
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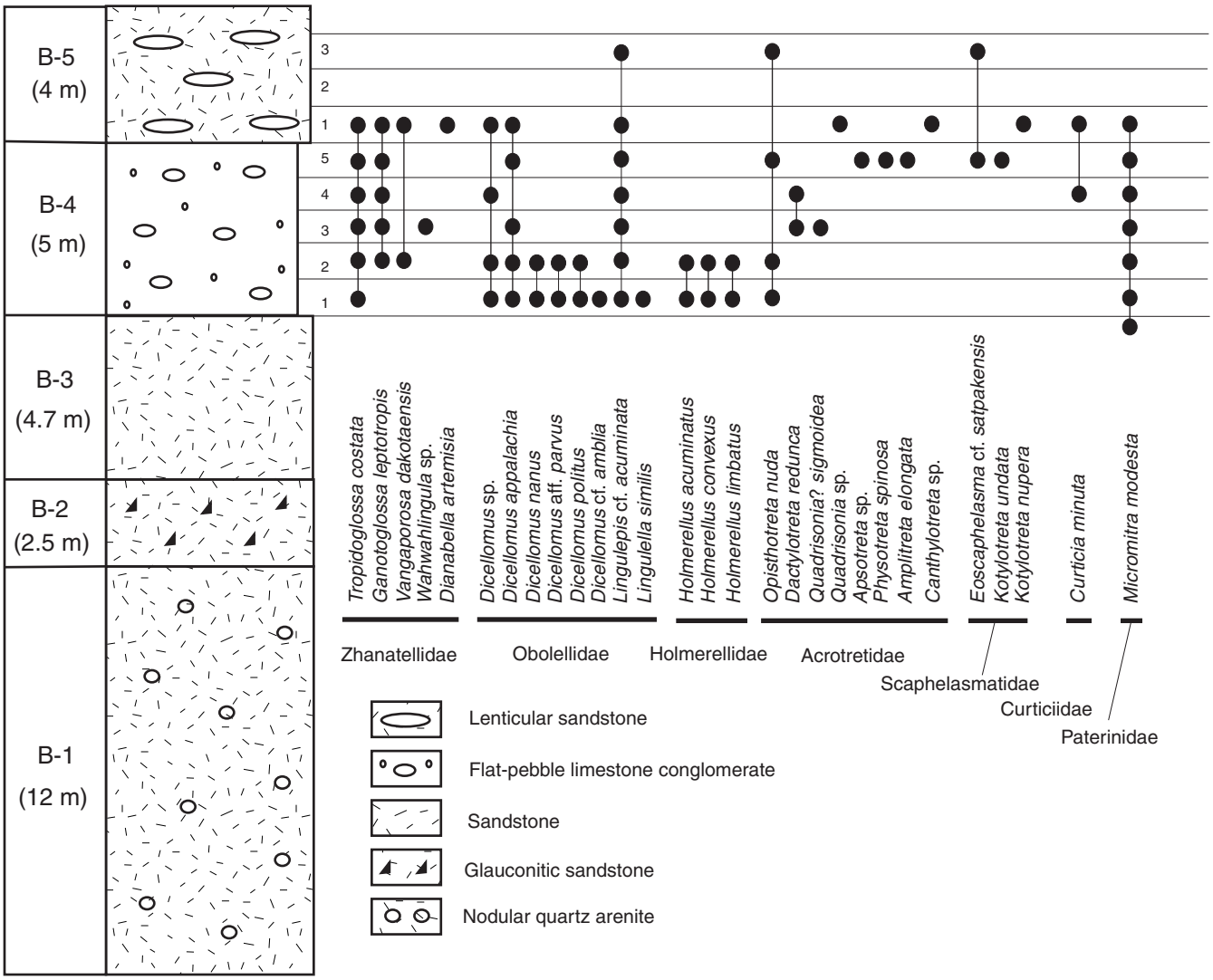
Obolidae
Acrotretidae
Curticiidae
Paterinidae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Tropidoglossa costata
Ganotoglossa leptotropis
Vangaporosa dakotaensis
Wahwahlingula sp.
Dianabella artemisia
Dicellomus sp.
Dicellomus appalachia
Dicellomus nanus
Dicellomus aff. parvus
Dicellomus politus
Dicellomus cf. amblia
Lingulepis cf. acuminata
Lingulella similis
Holmerellus acuminatus
Holmerellus convexus
Holmerellus limbatus
Opisthotreta nuda
Dactylotreta reducta
Quadrisonia? sigmoidea
Quadrisonia sp.
Apsotreta sp.
Physotreta spinosa
Amplitreta elongata
Canthylotreta sp.
Eoscaphelasma cf. satpakensis
Kotylotreta undata
Kotylotreta nupera
Curticia minuta
Micromitra modesta
Zhanatellidae
Obolellidae
Holmerellidae
Acrotretidae
Scaphelasmatidae
Curticiidae
Paterinidae
Lenticular sandstone
Flat-pebble limestone conglomerate
Sandstone
Glauconitic sandstone
Nodular quartz arenite

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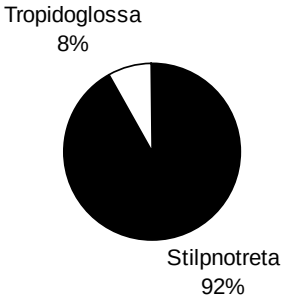

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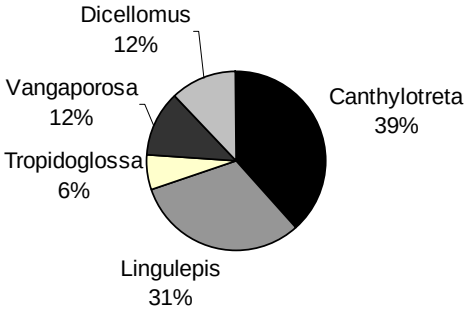

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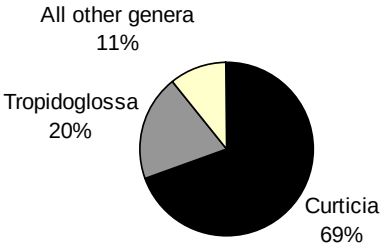

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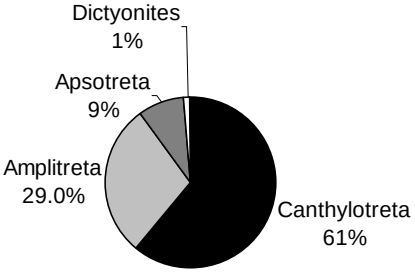

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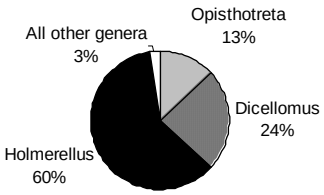

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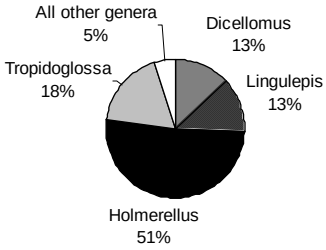

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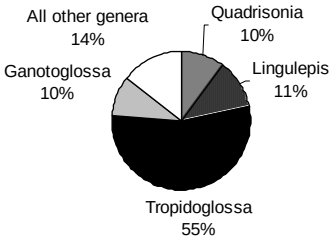

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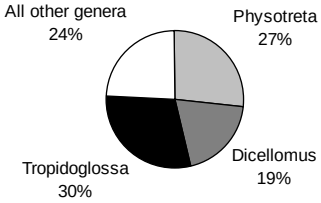

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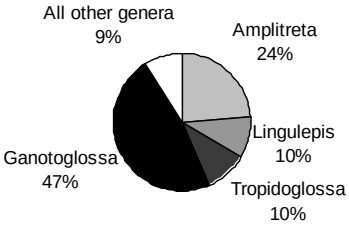

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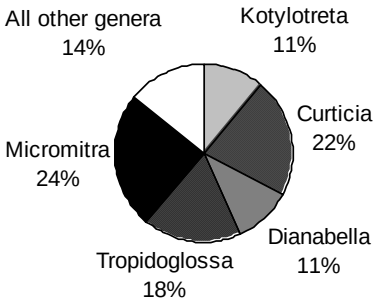
All other genera
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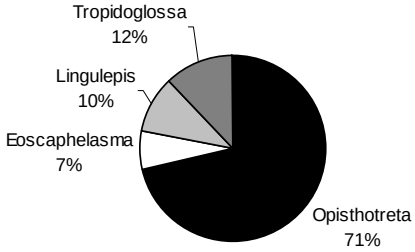
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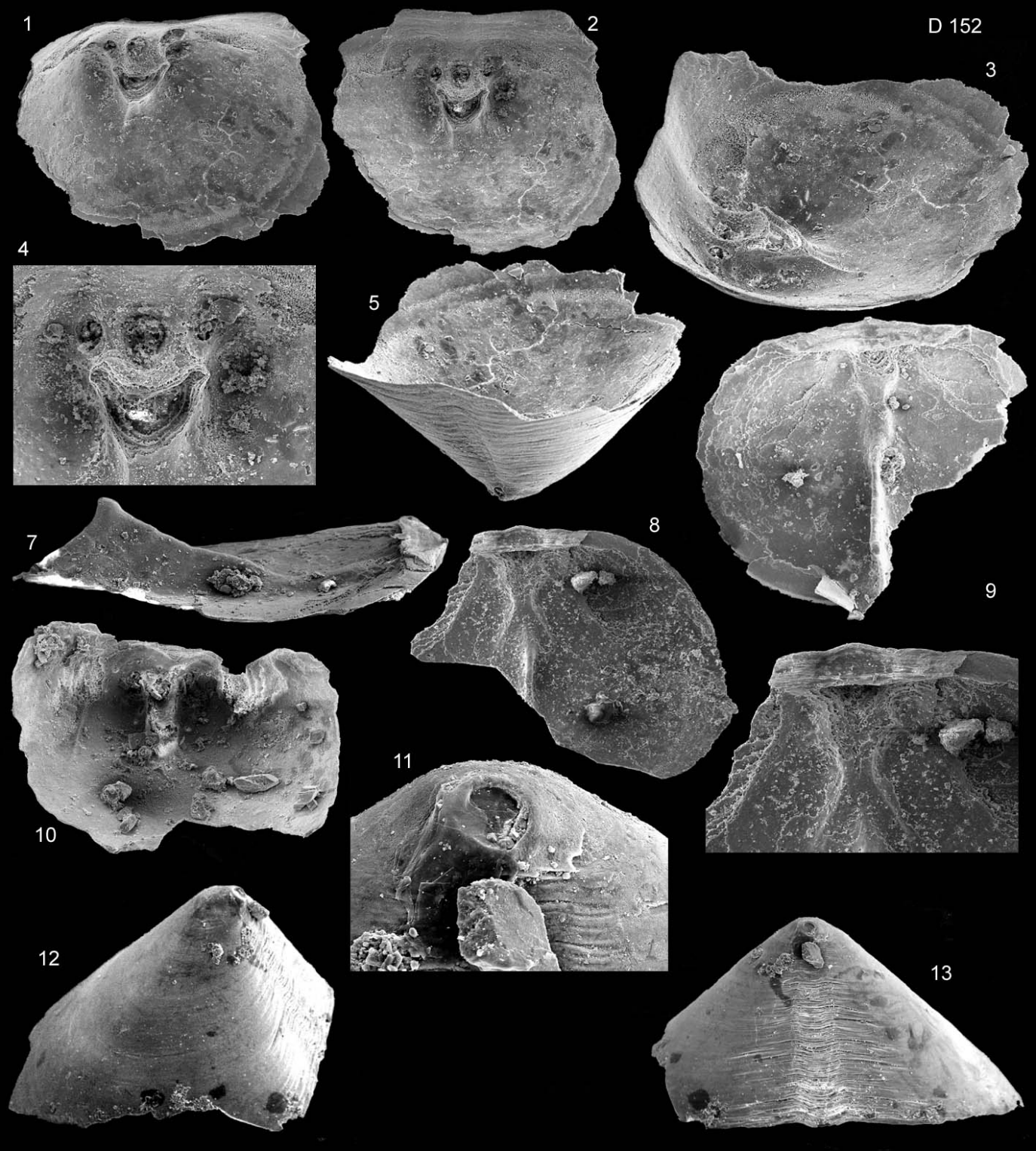
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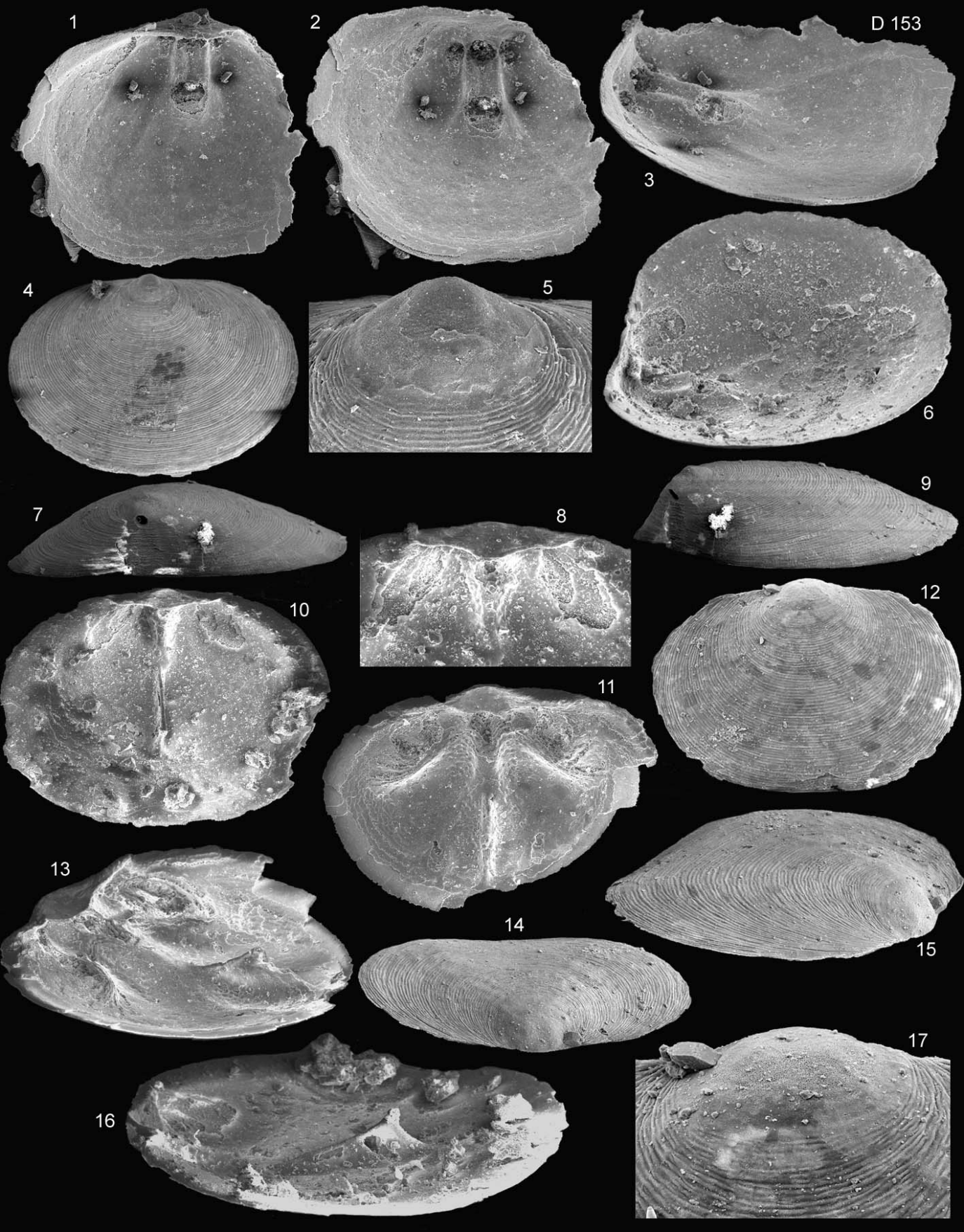
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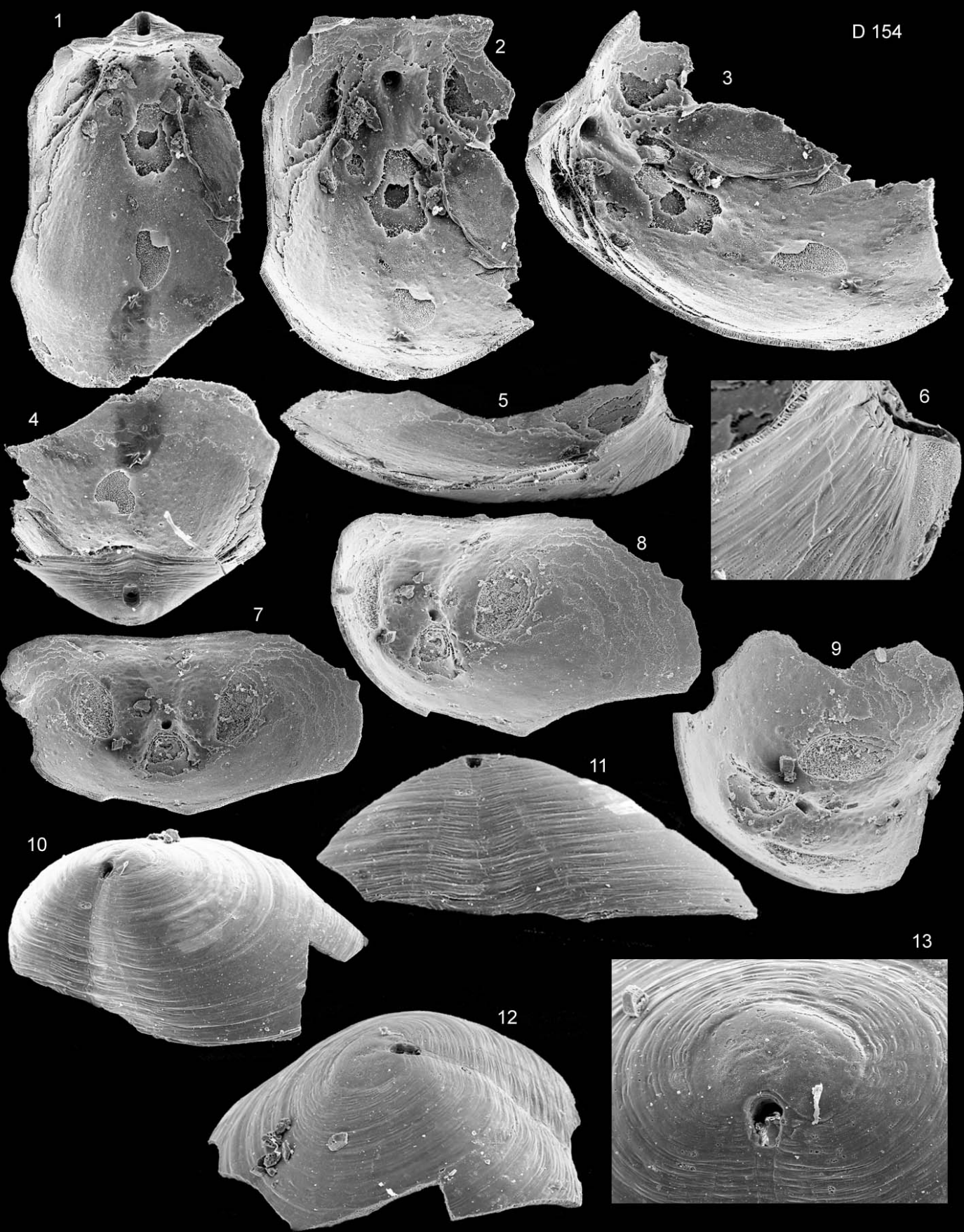
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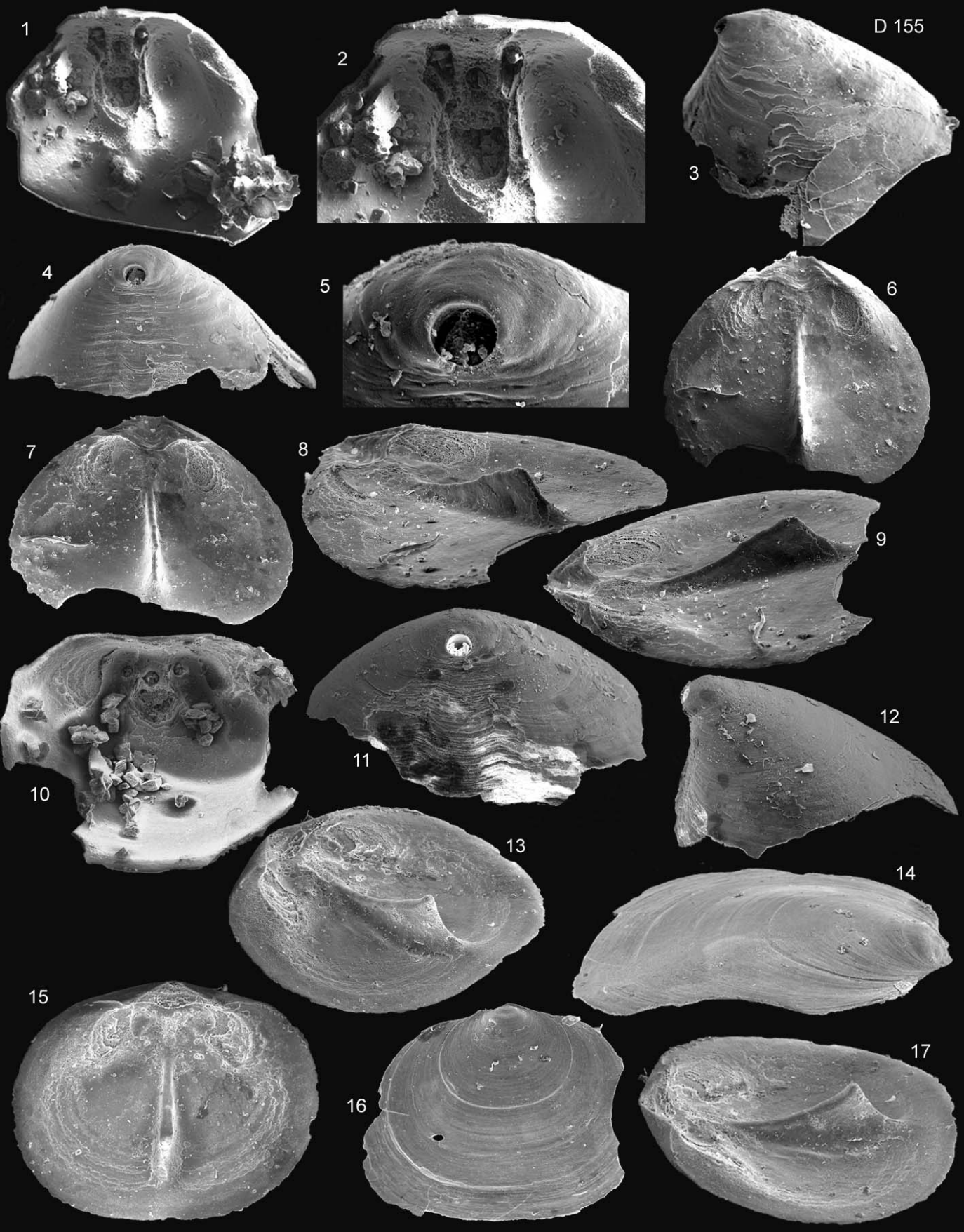
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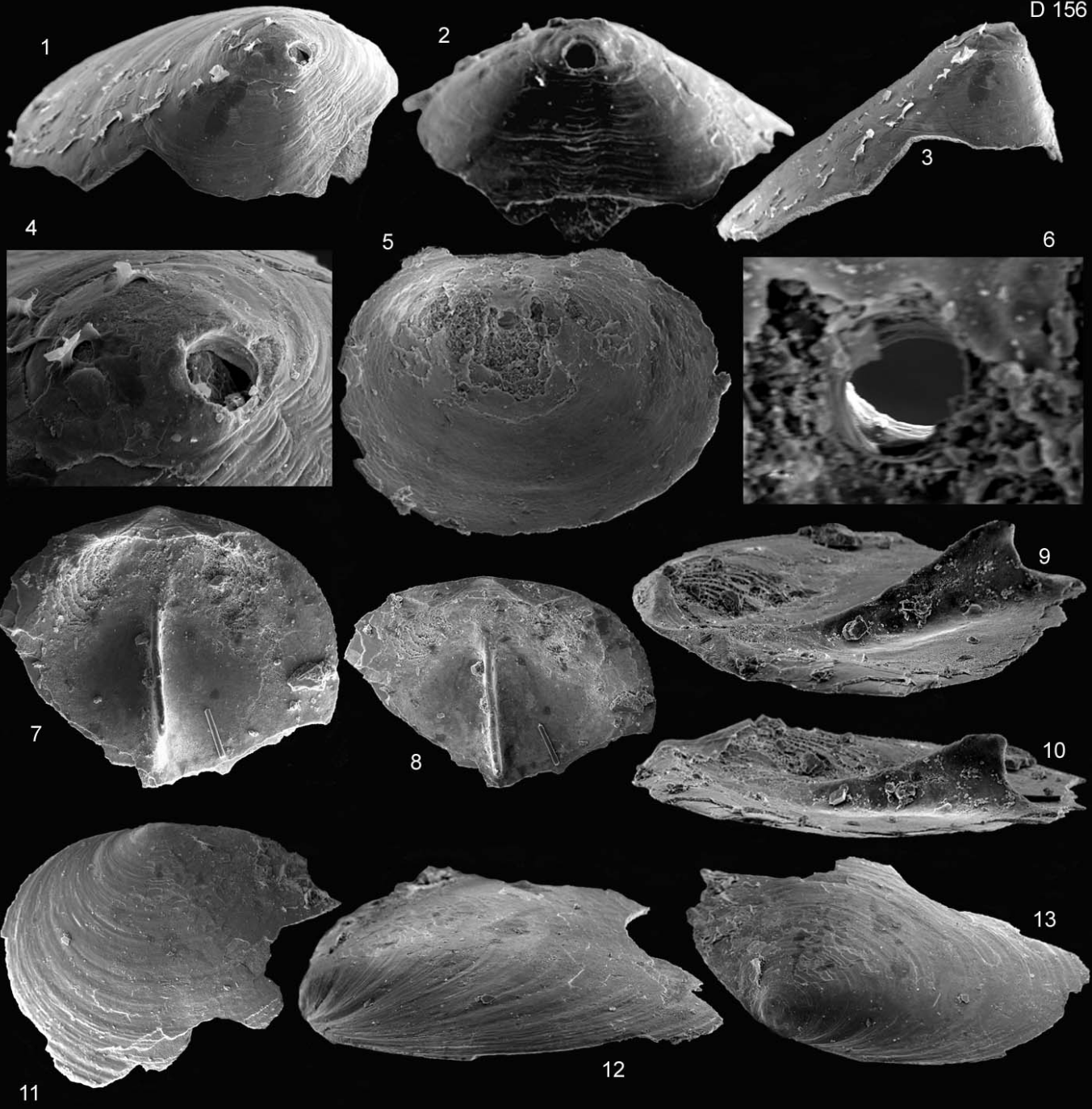
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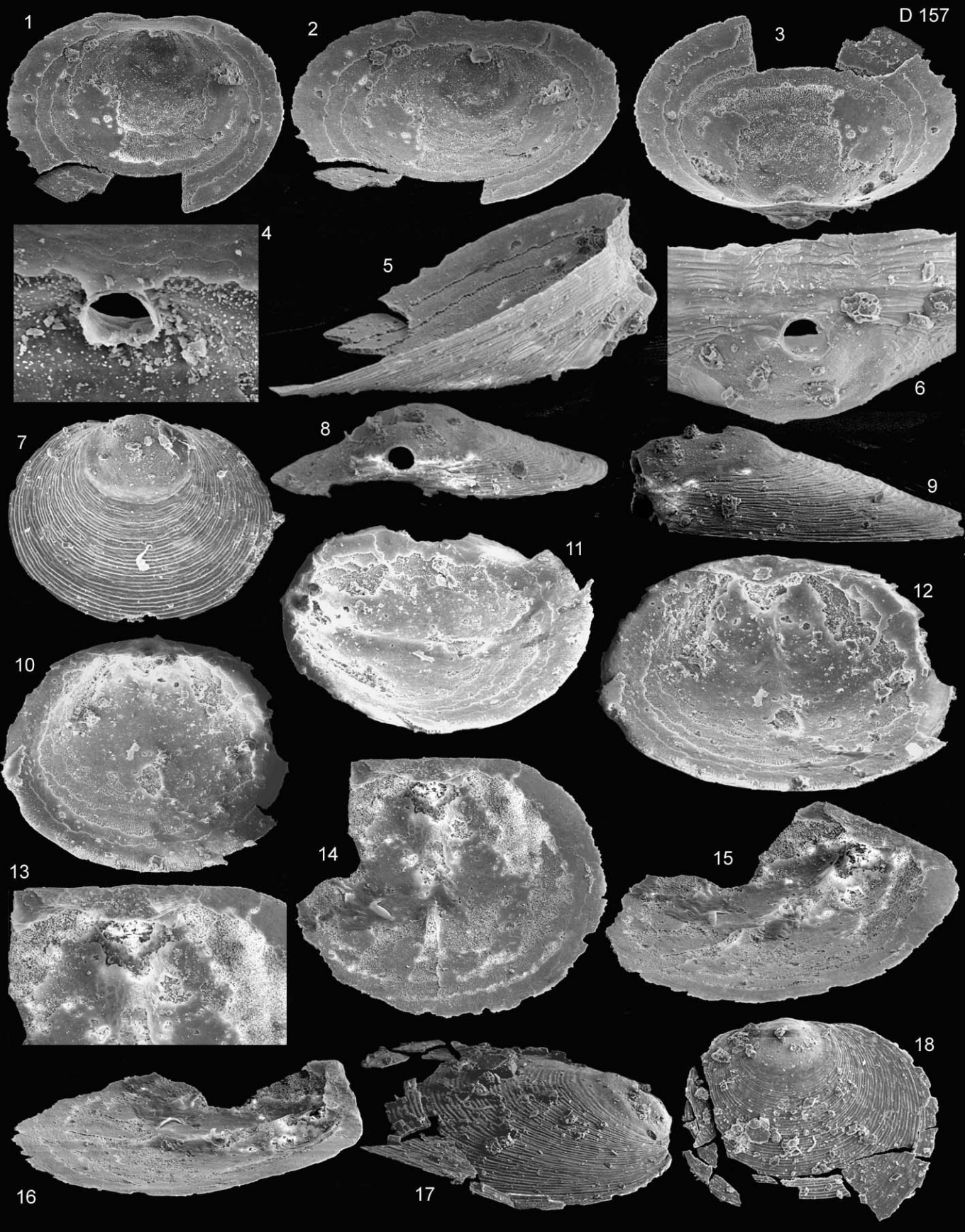
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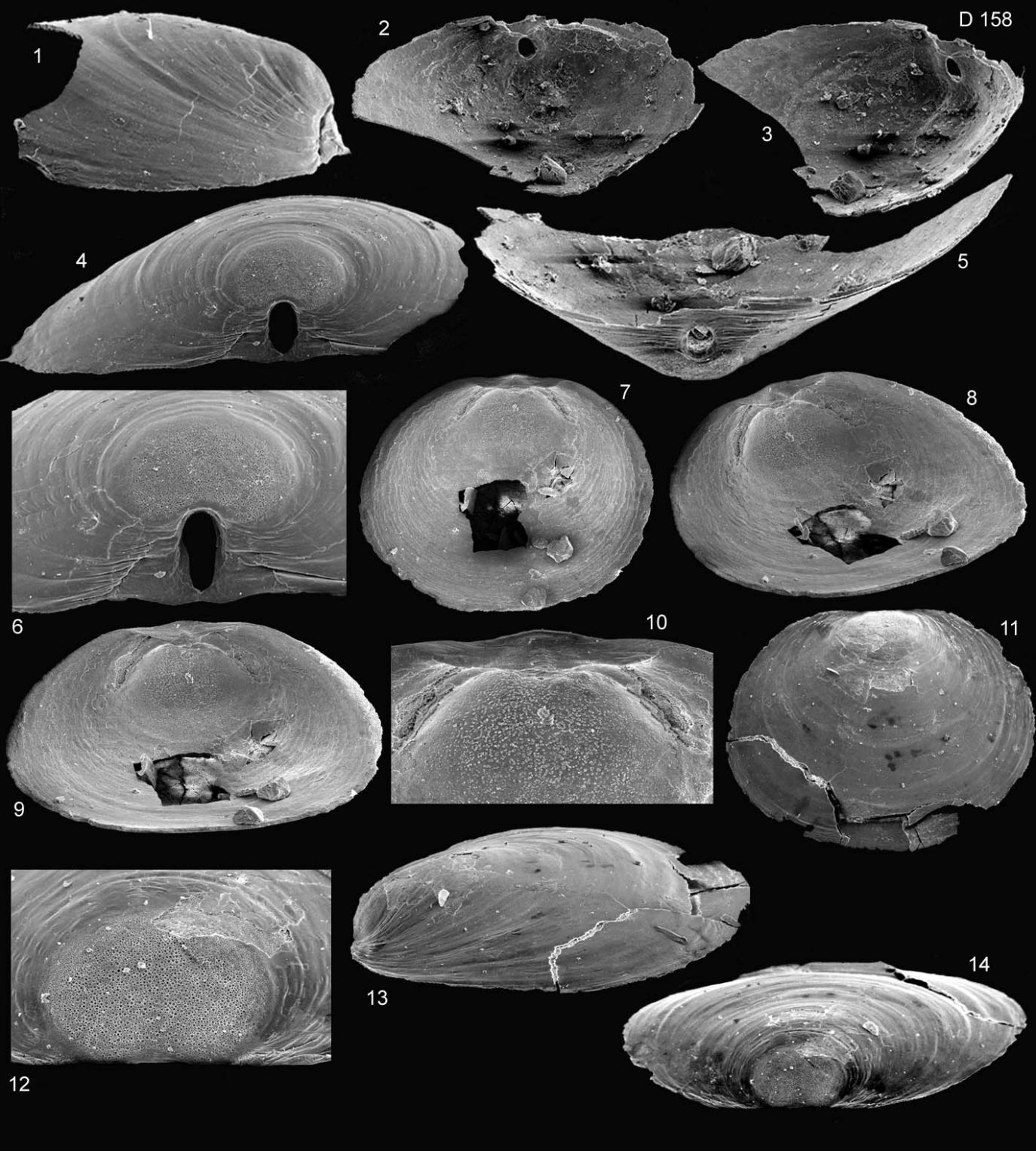
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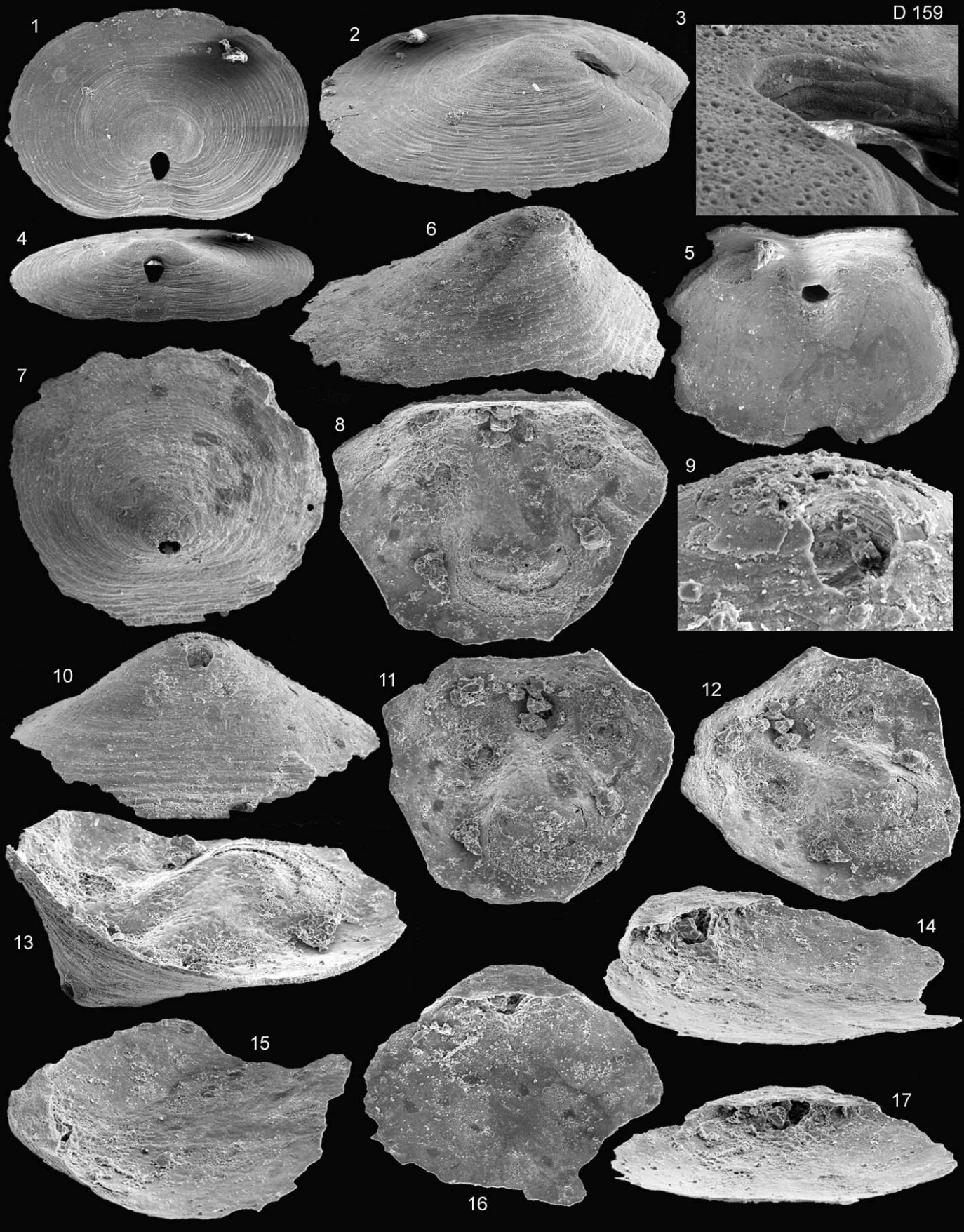
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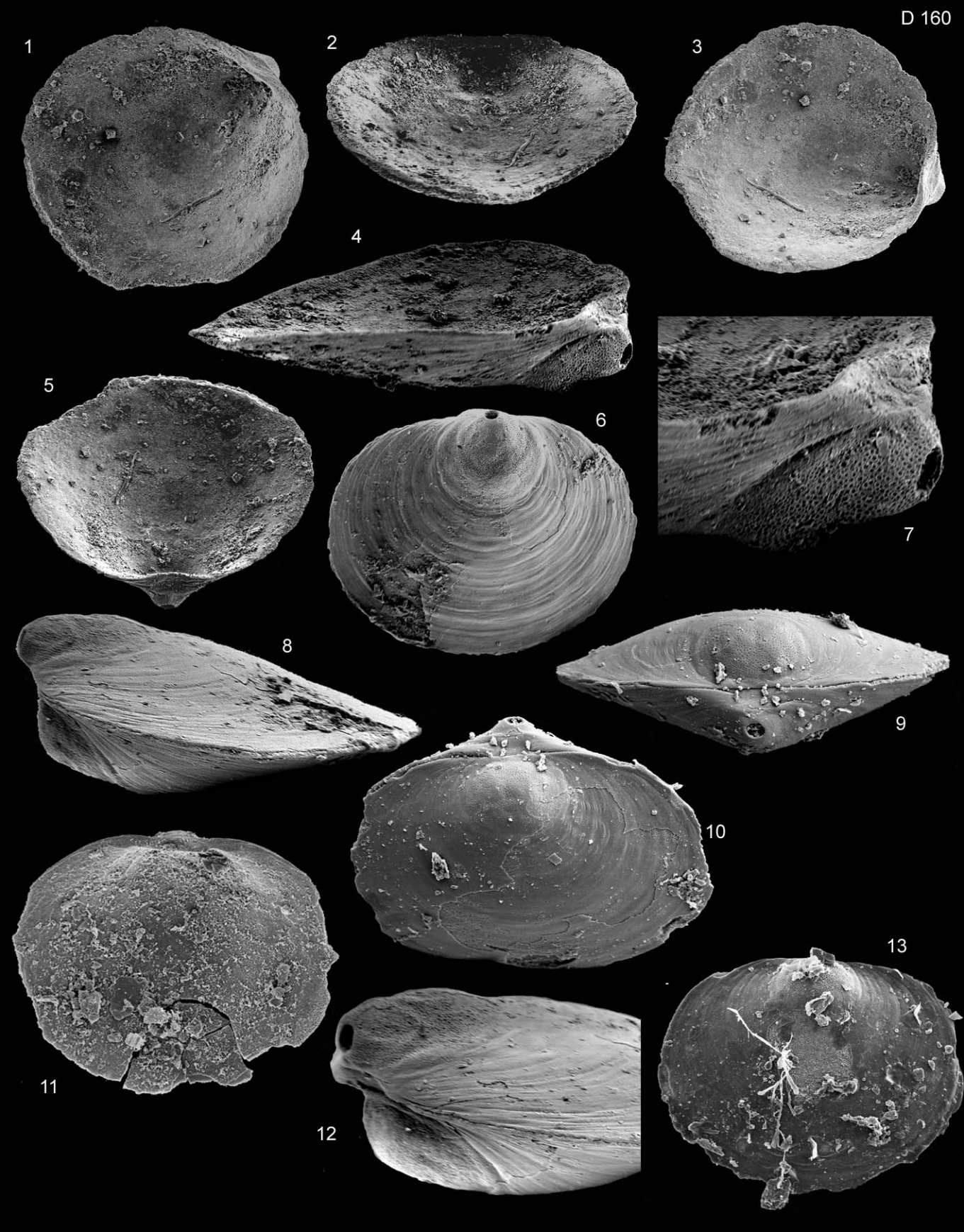
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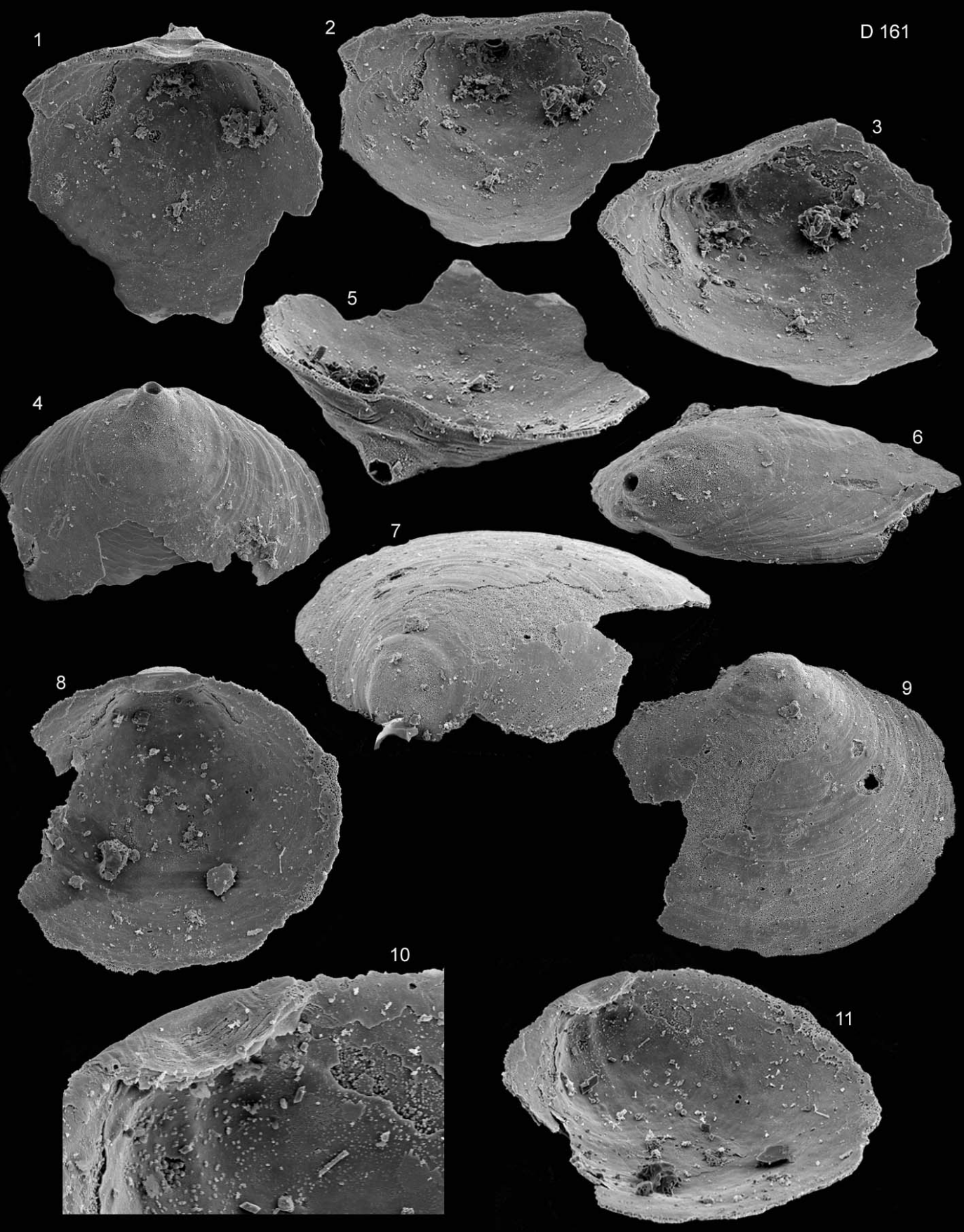
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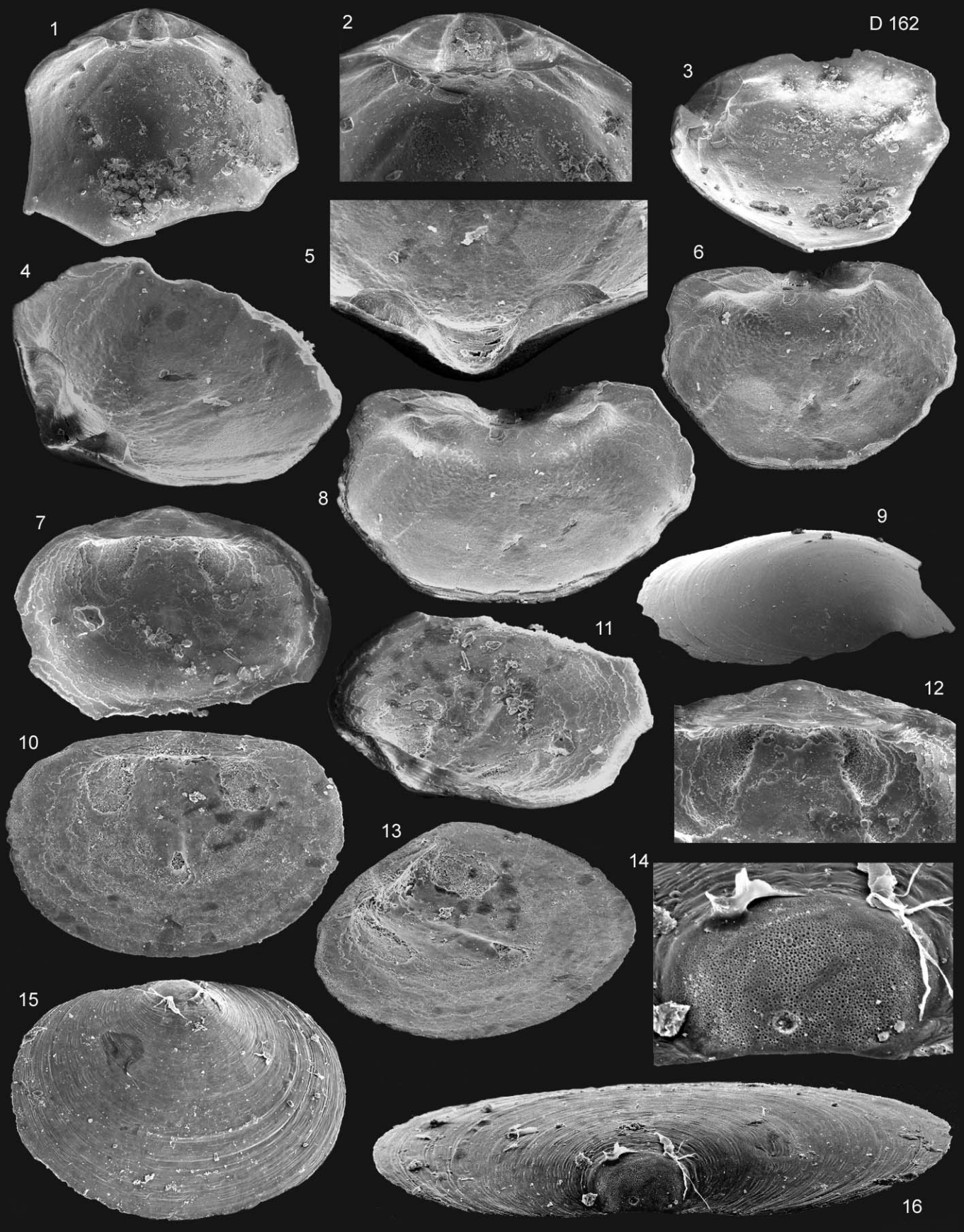
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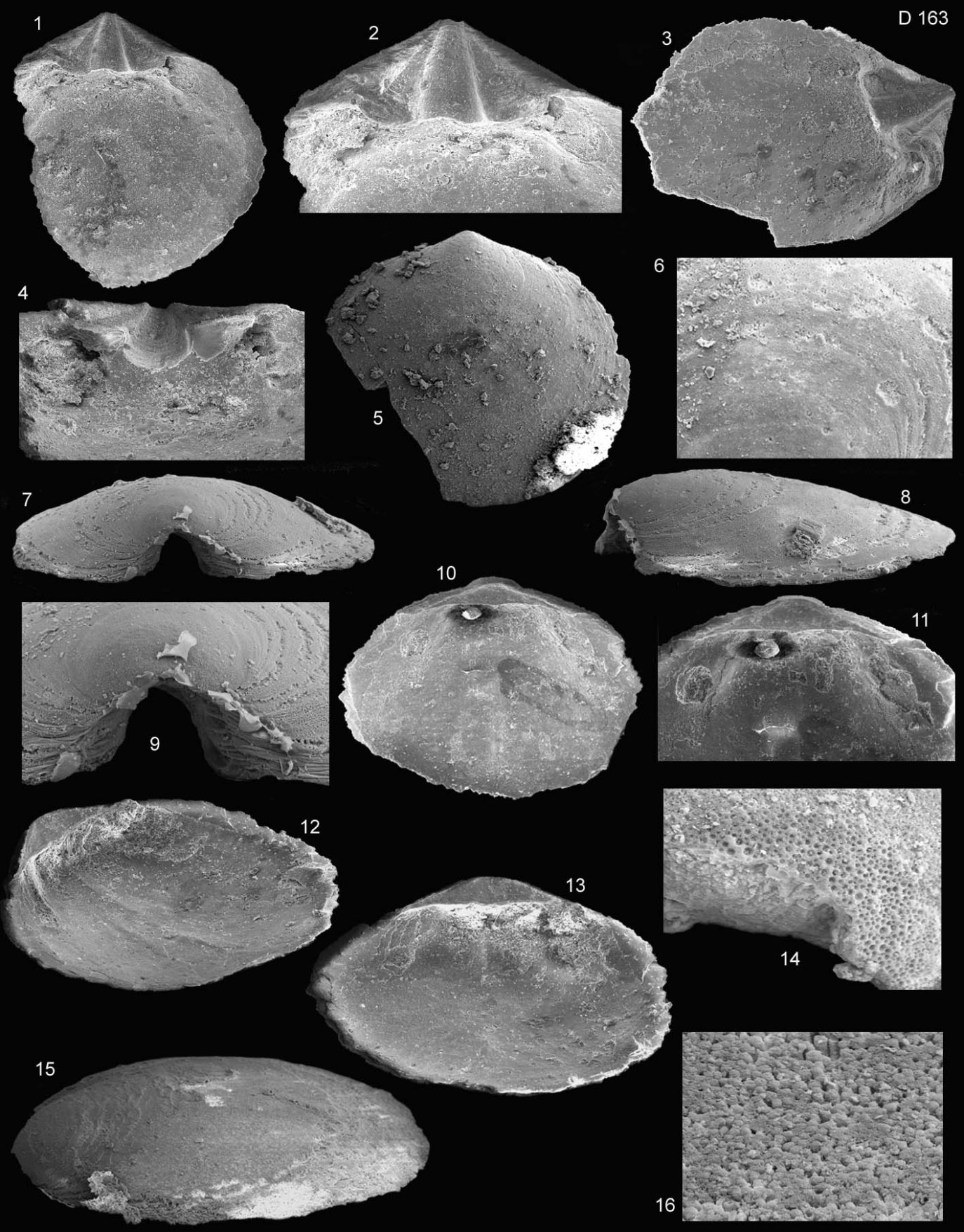
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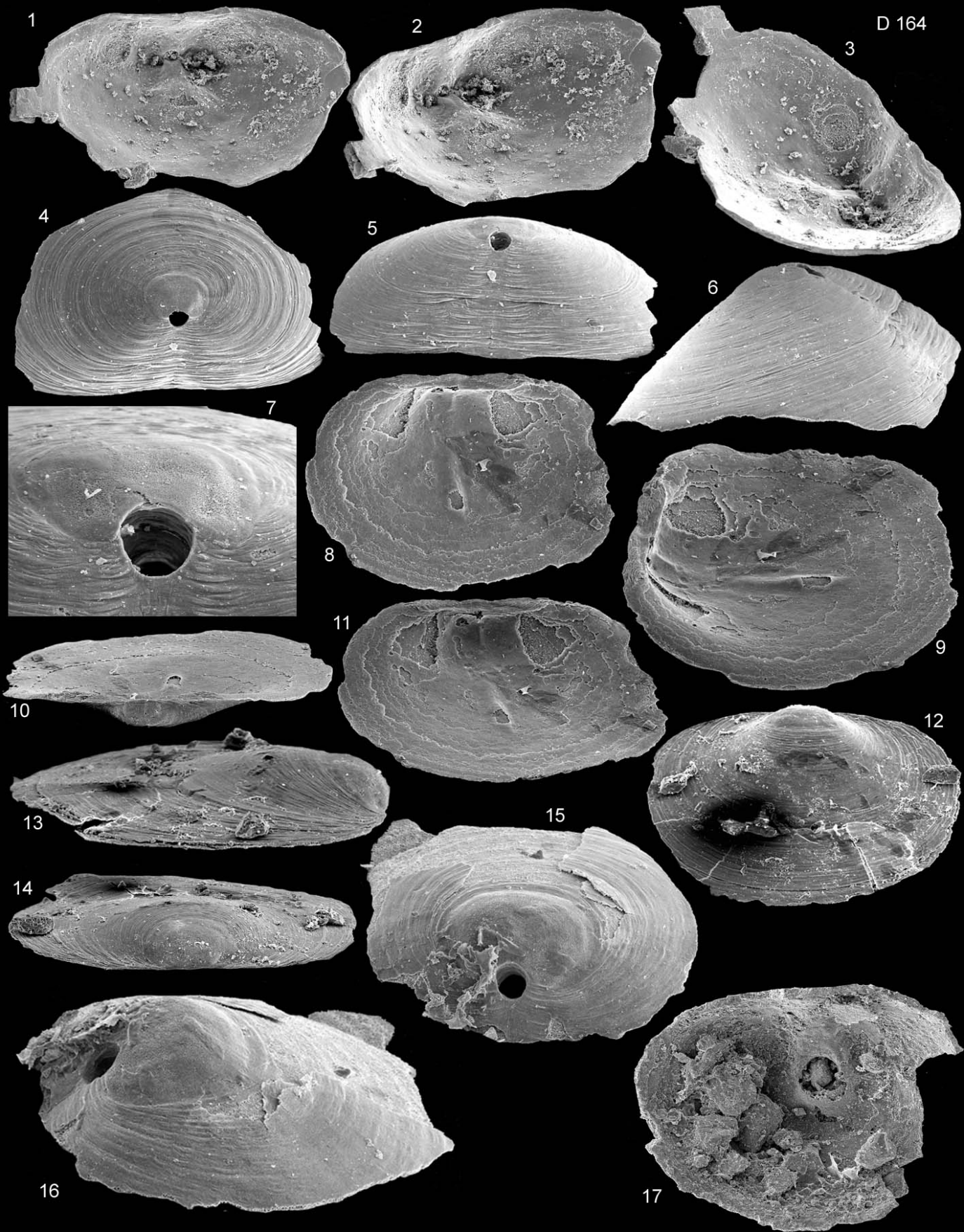
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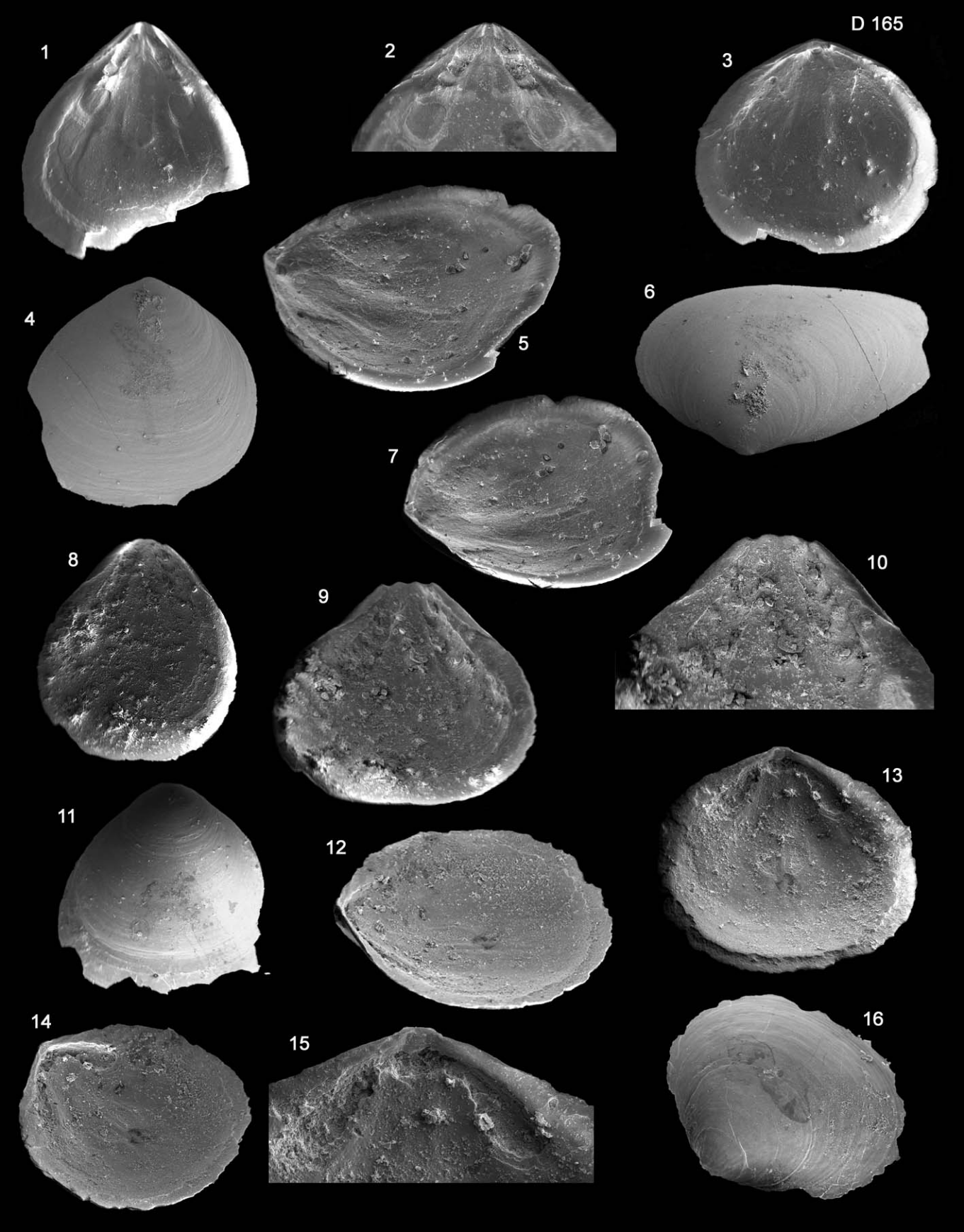
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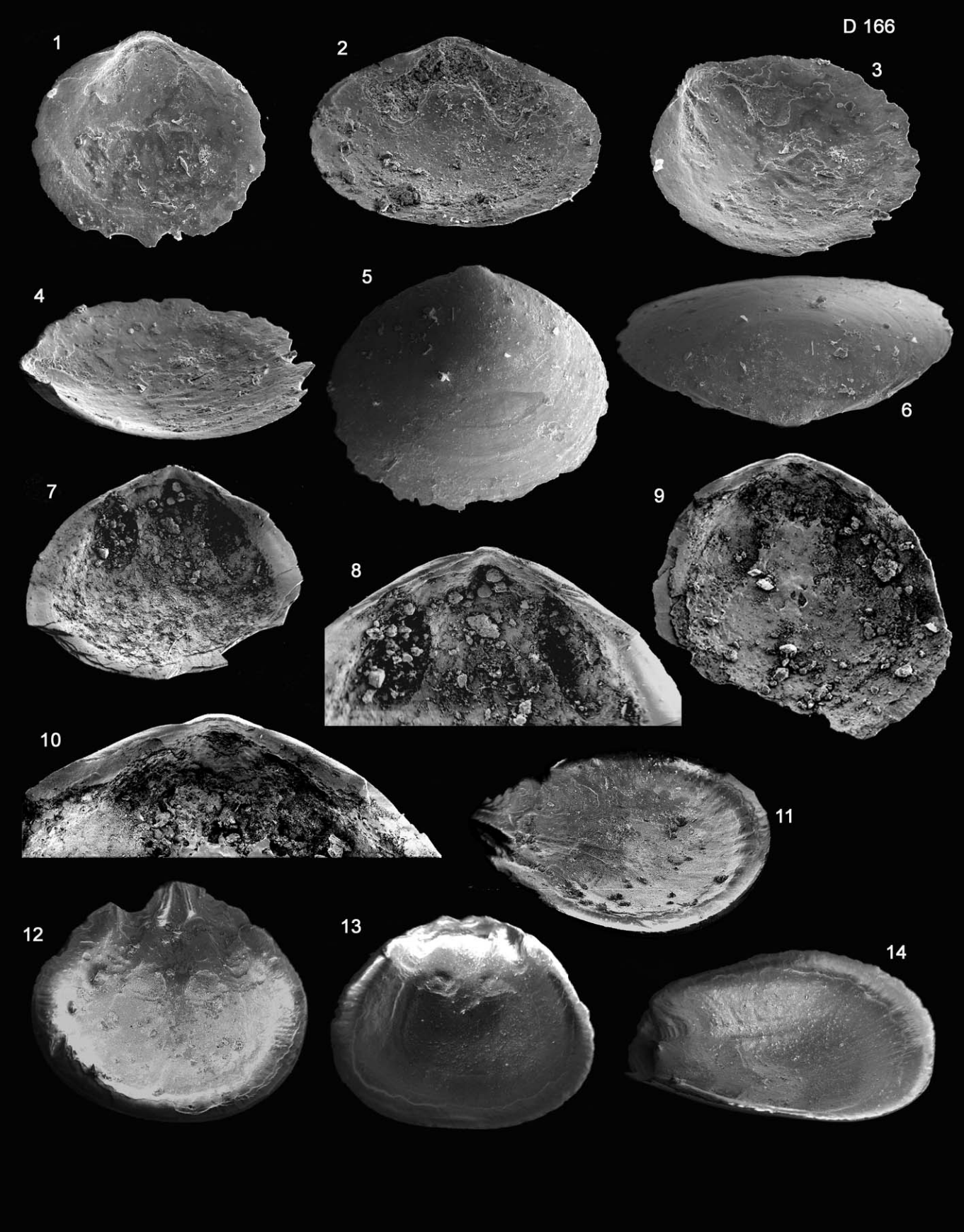
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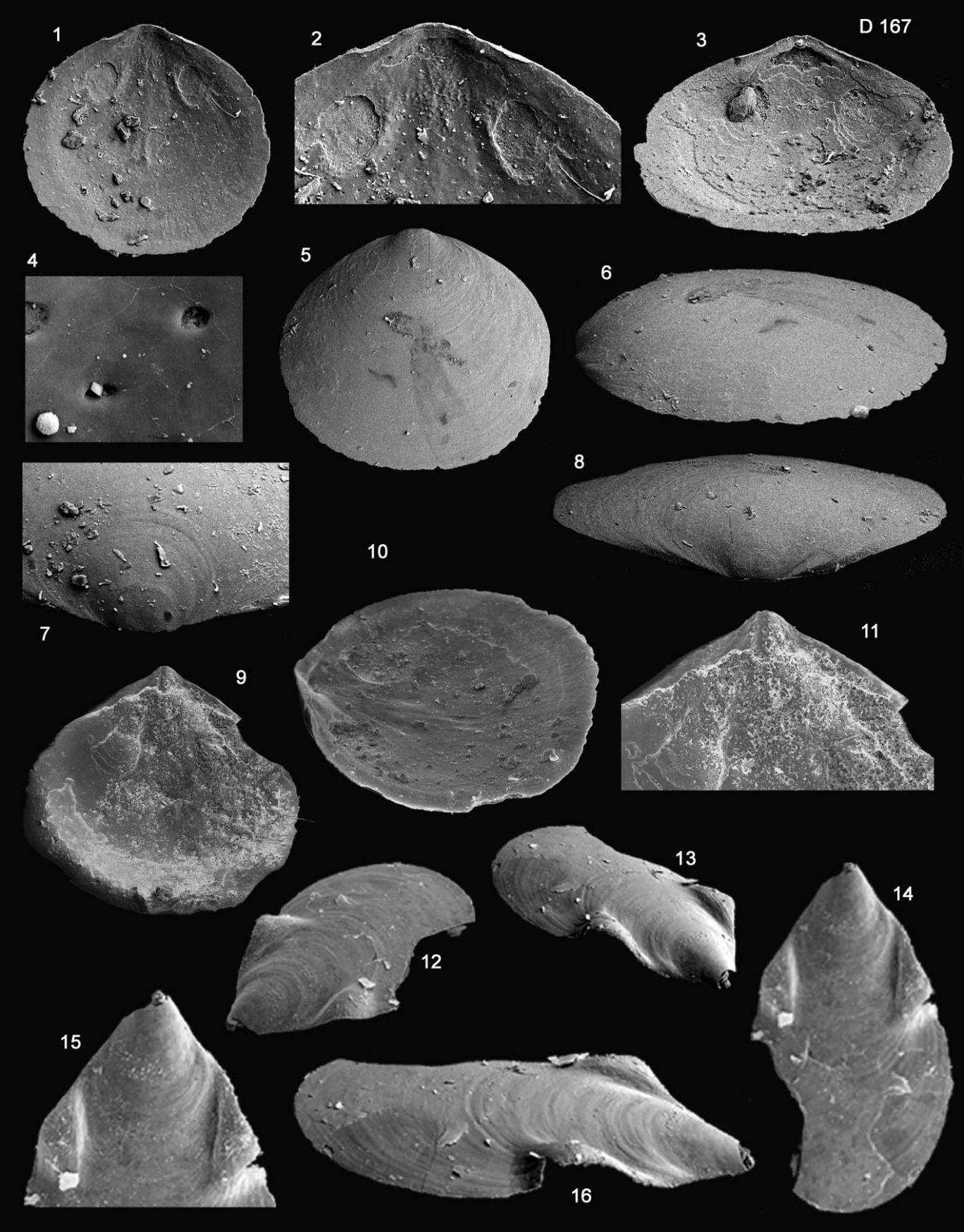
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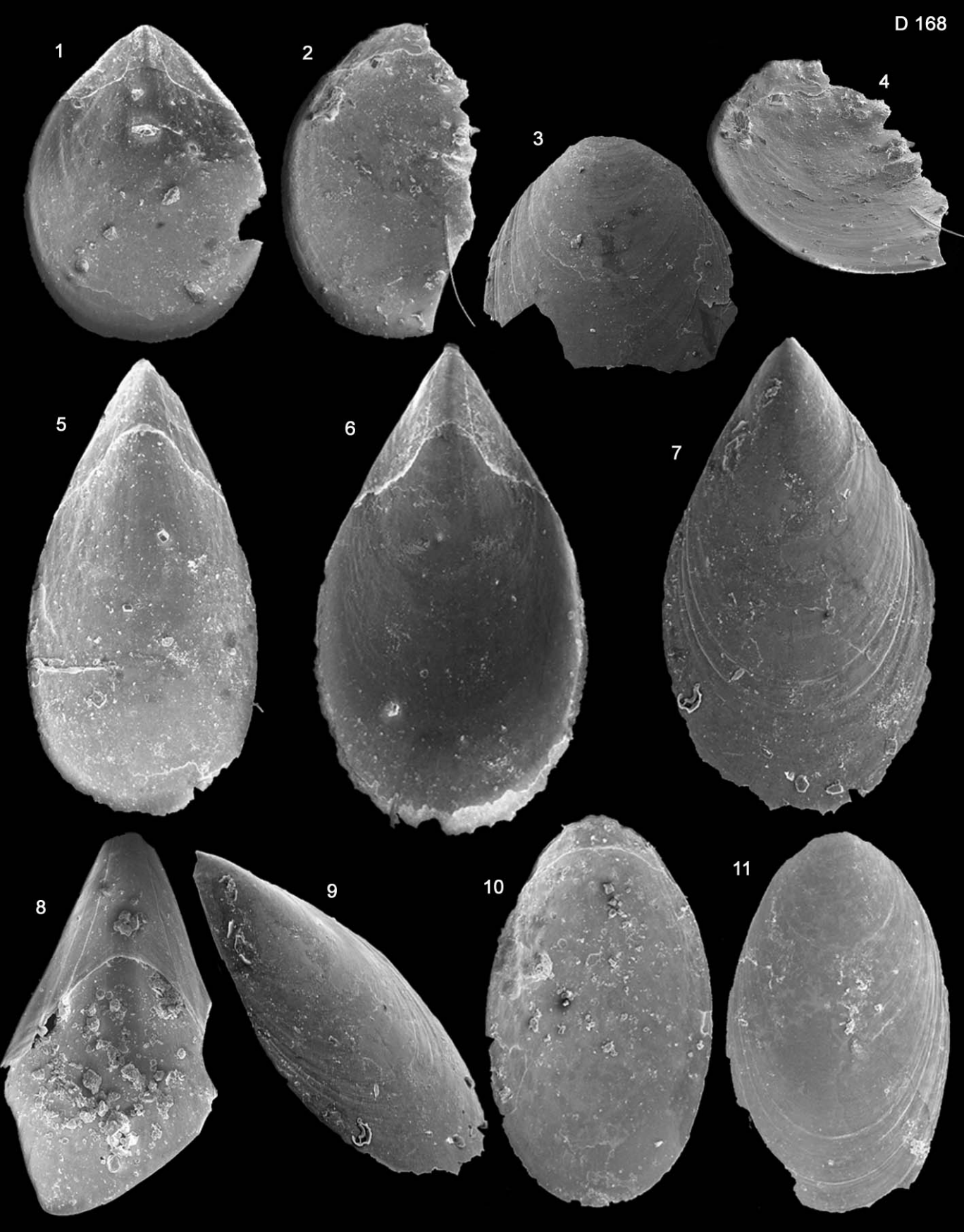
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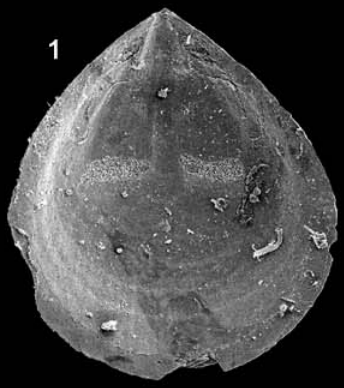
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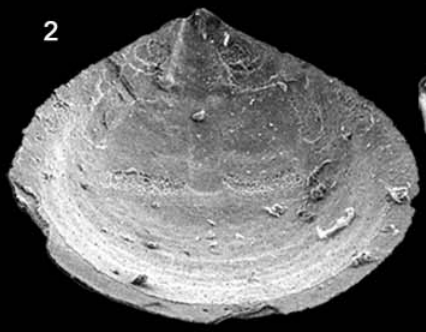
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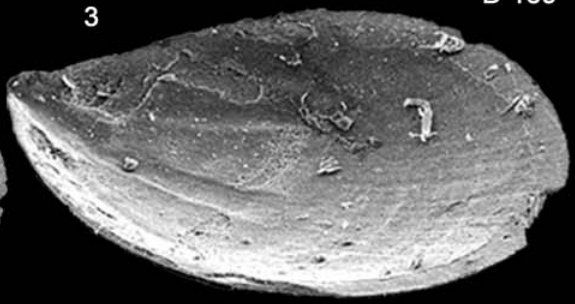
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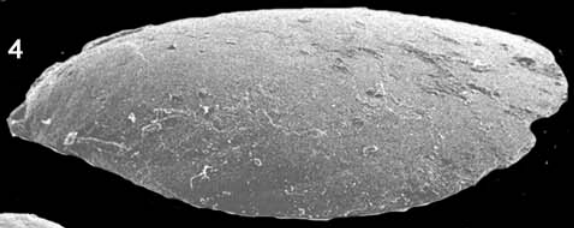
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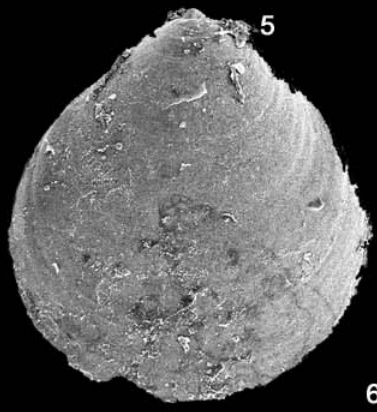
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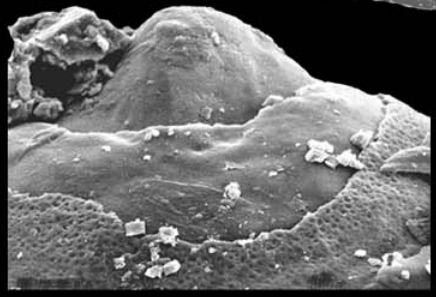
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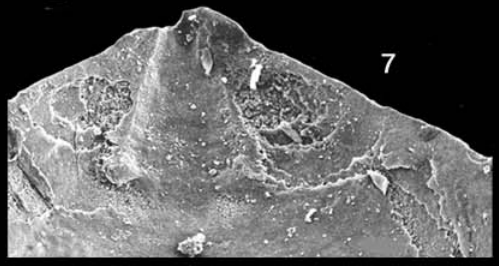
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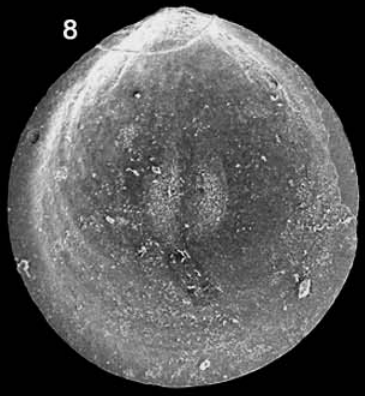
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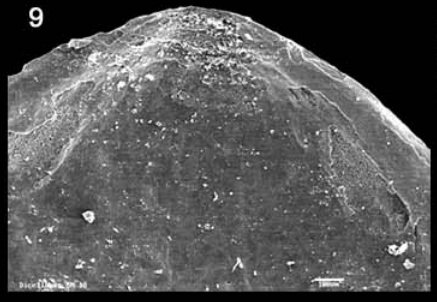
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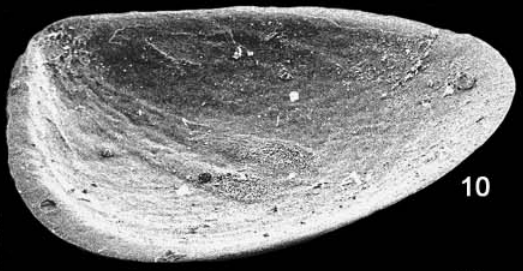
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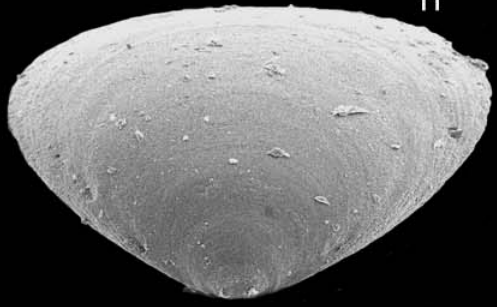
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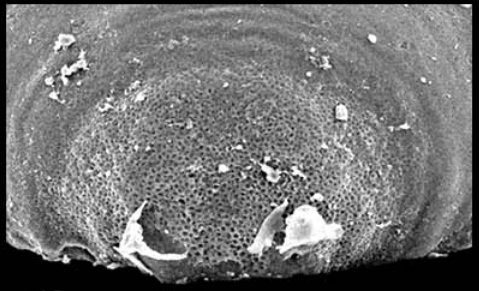
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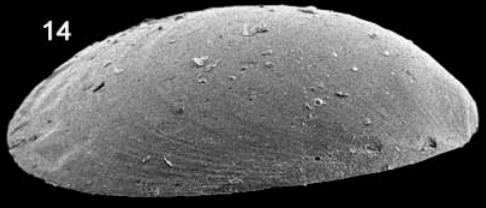
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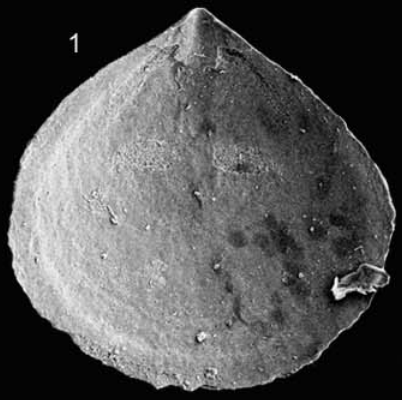
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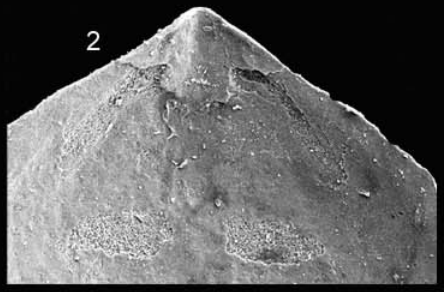
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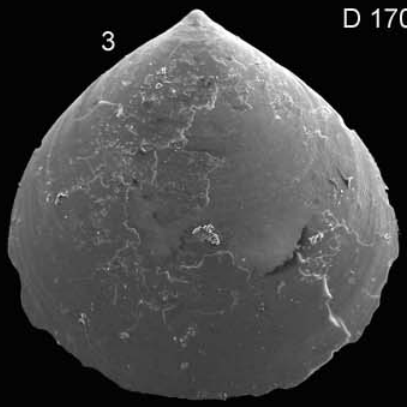
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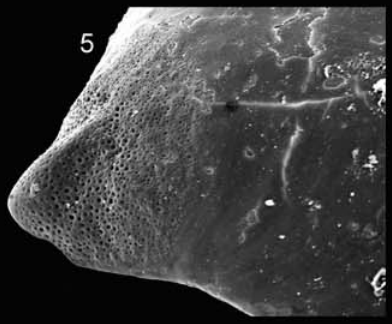
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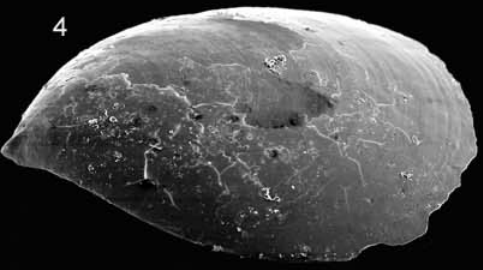
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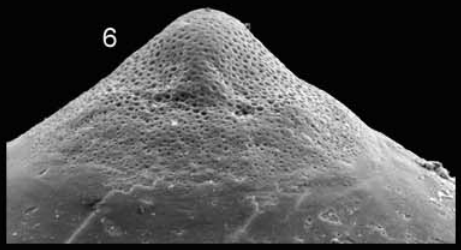
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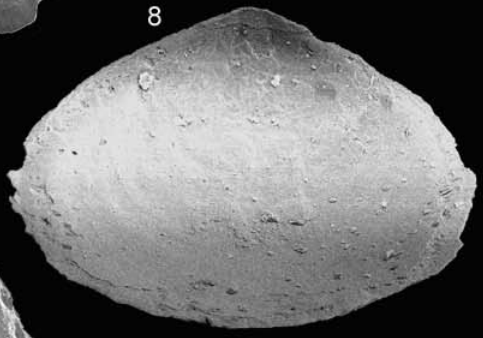
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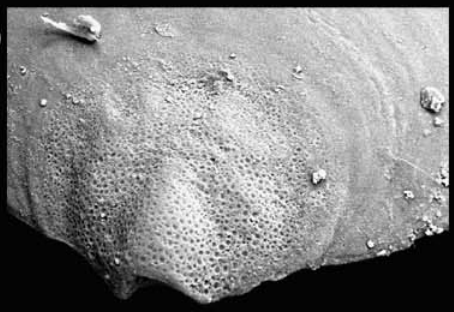
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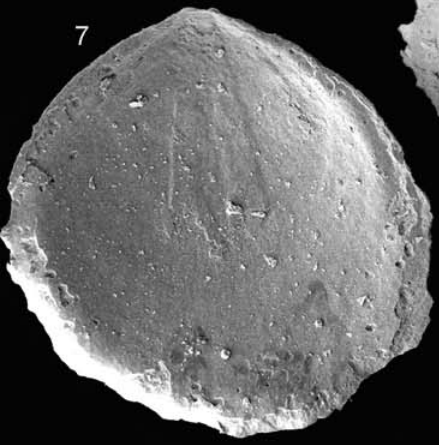
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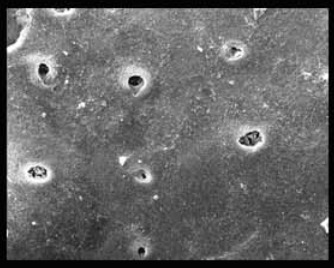
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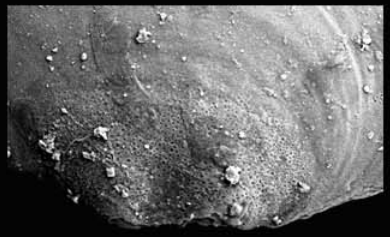
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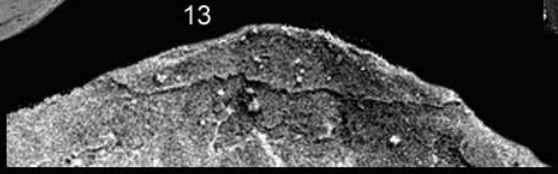
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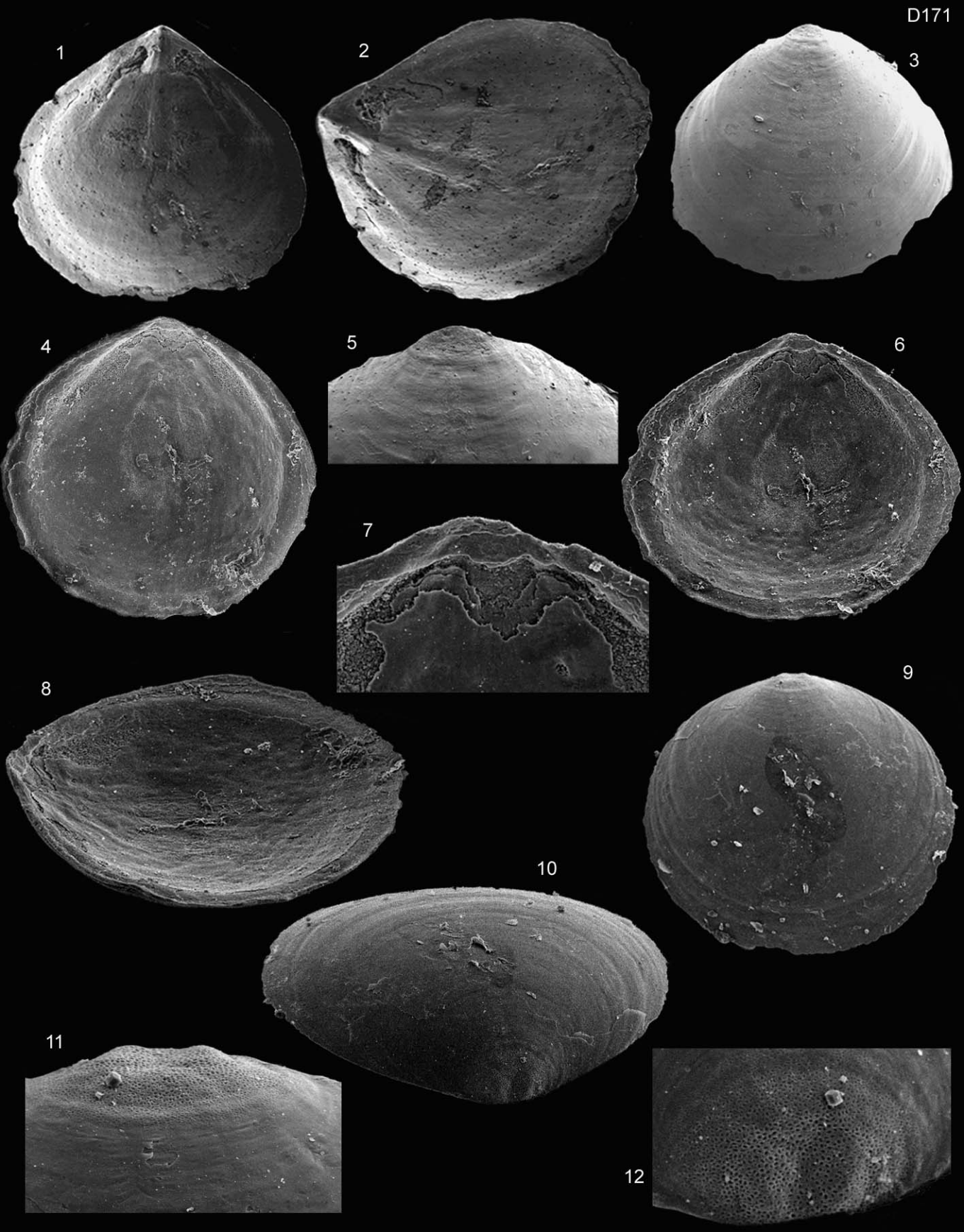
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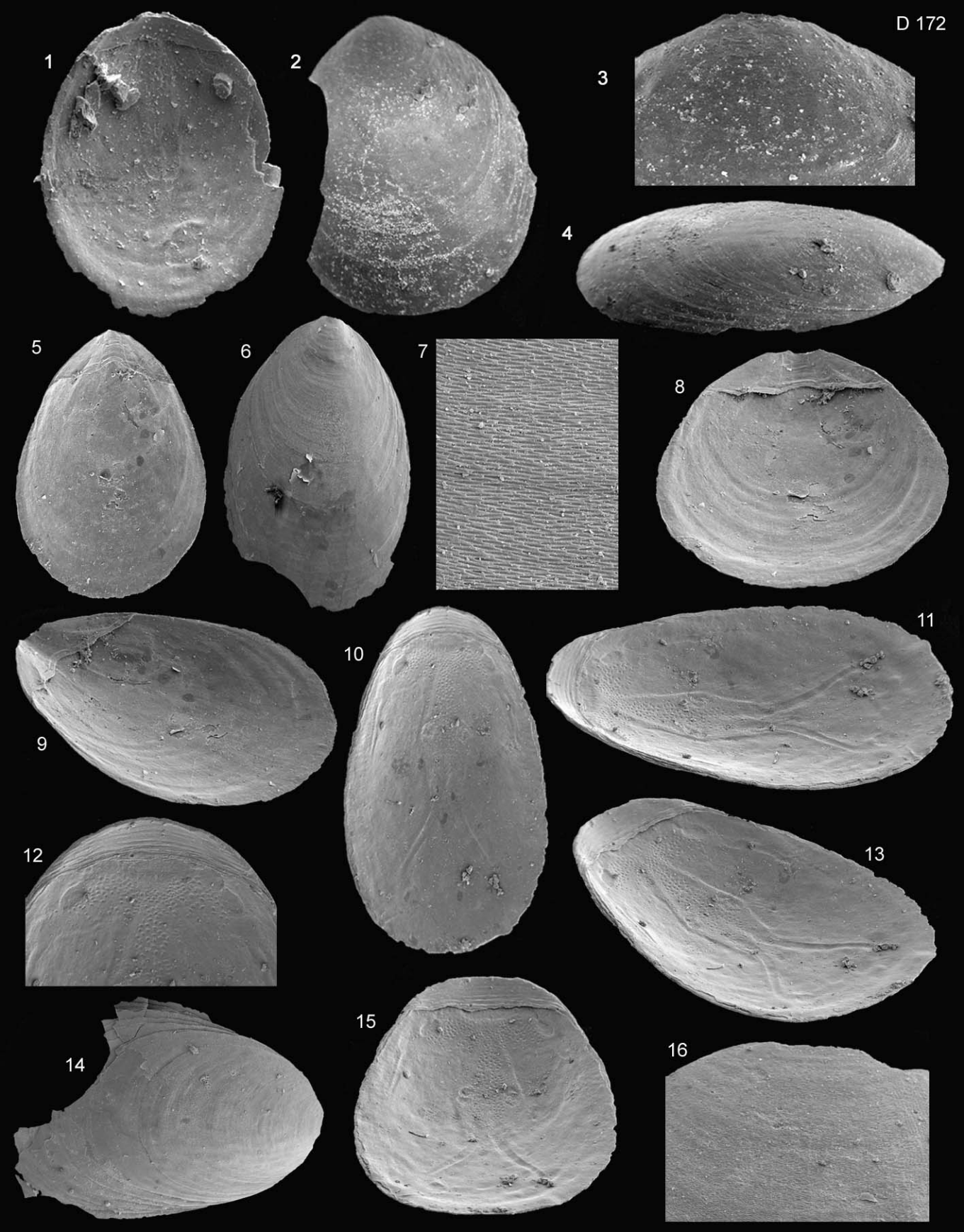
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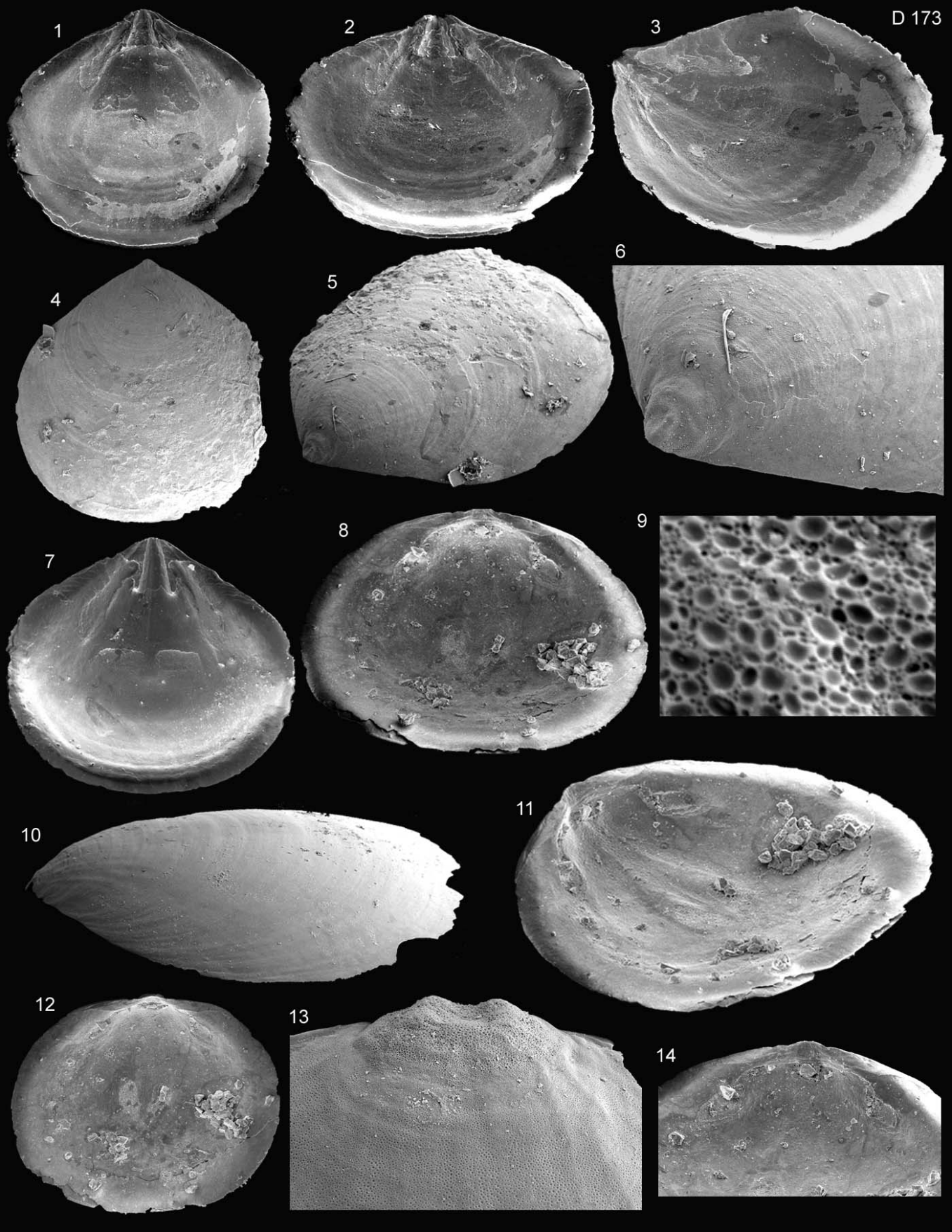
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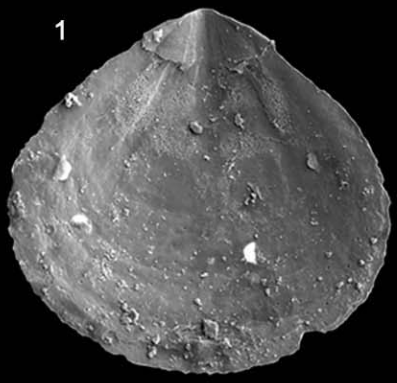
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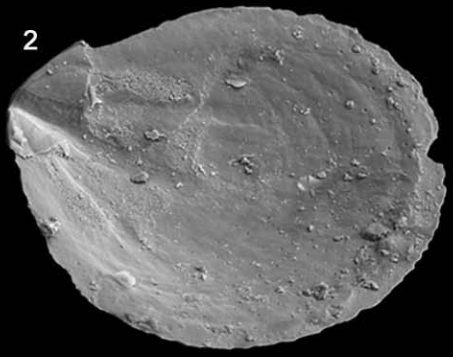
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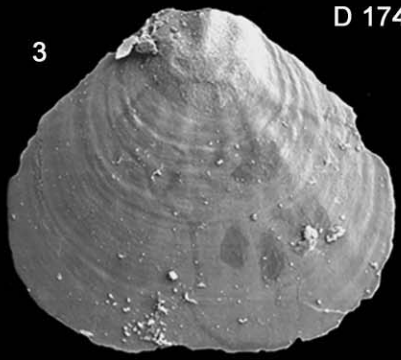
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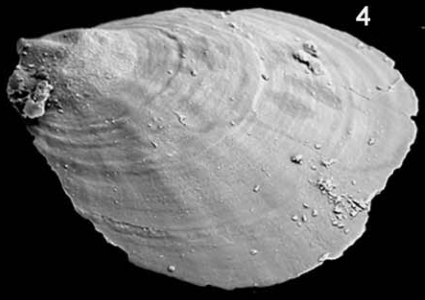
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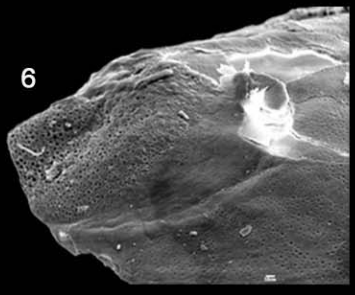
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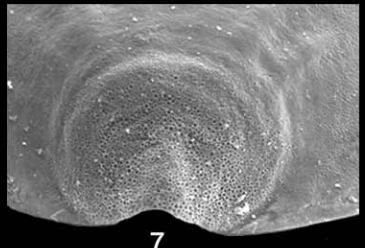
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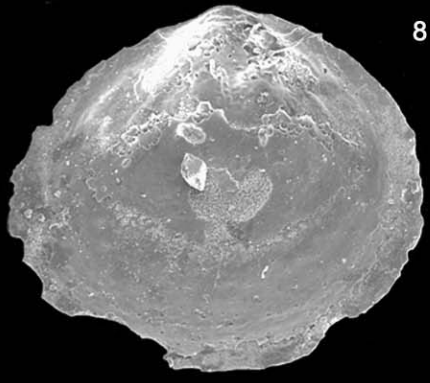
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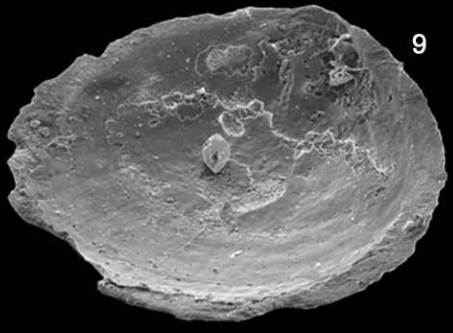
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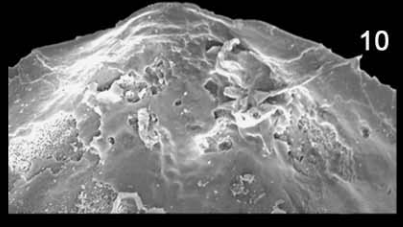
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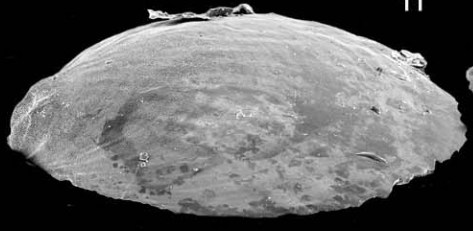
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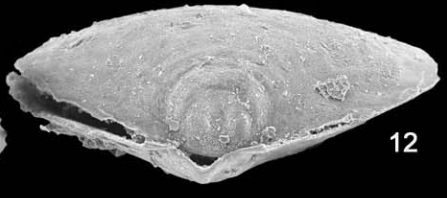
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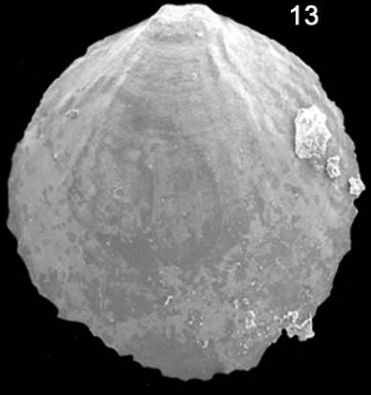
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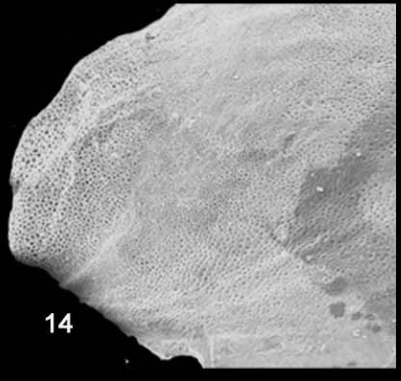
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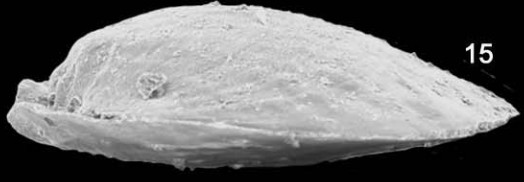
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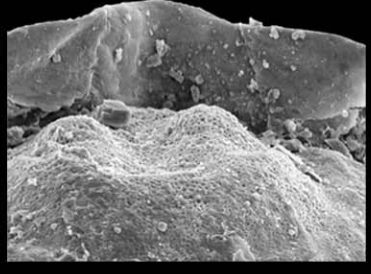
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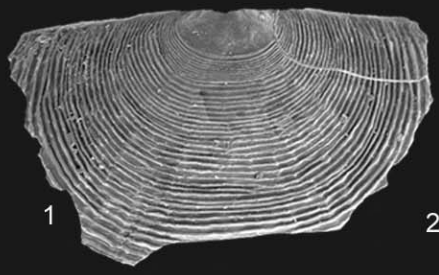
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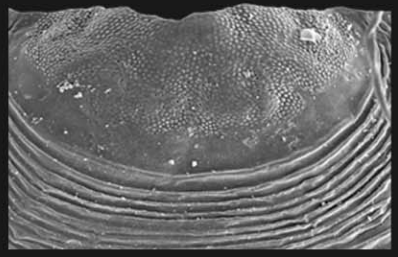
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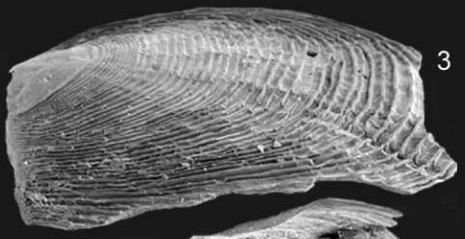
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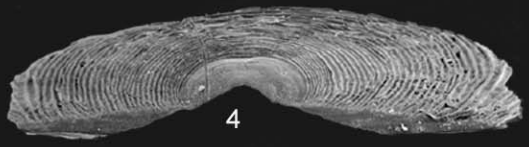
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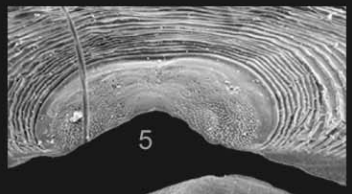
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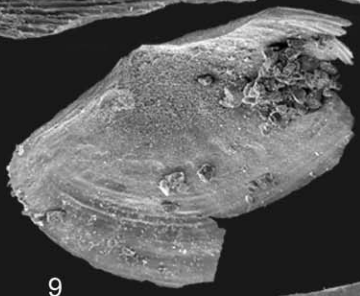
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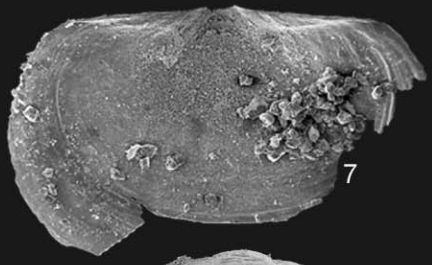
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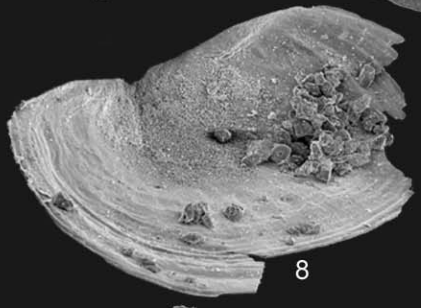
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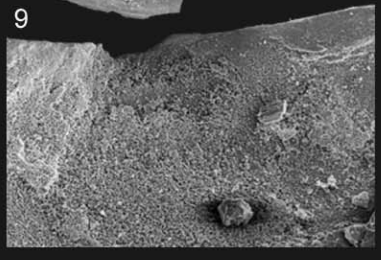
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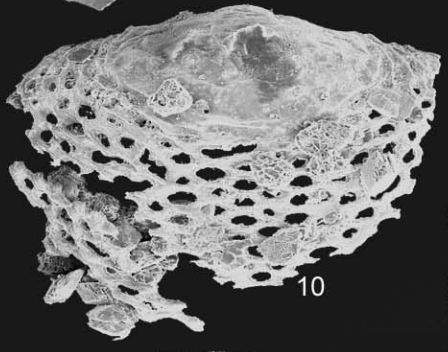
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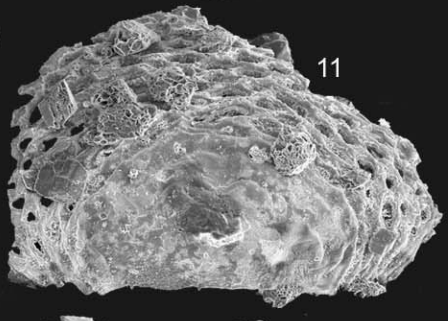
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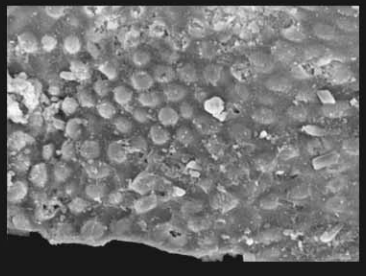

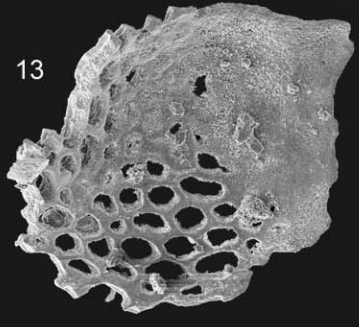
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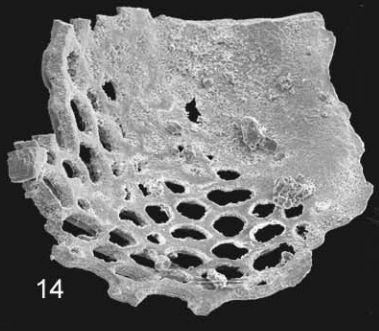
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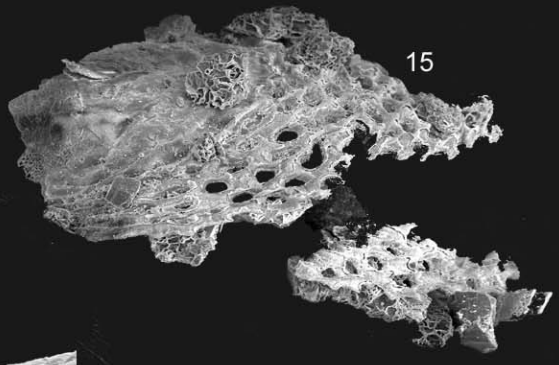
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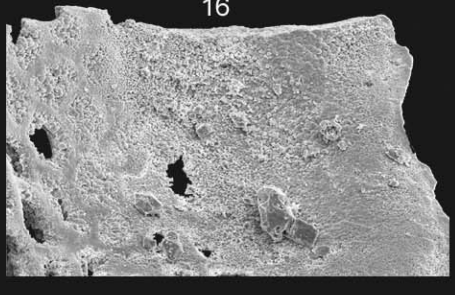

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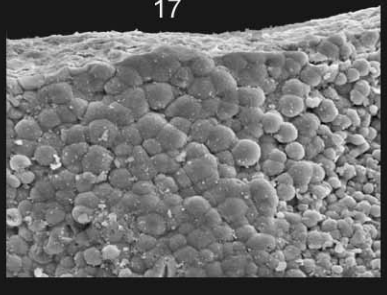

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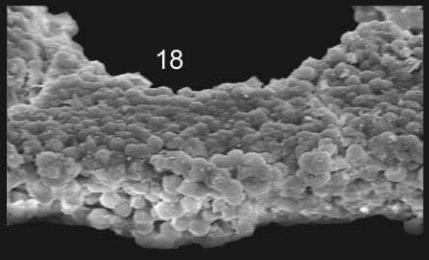

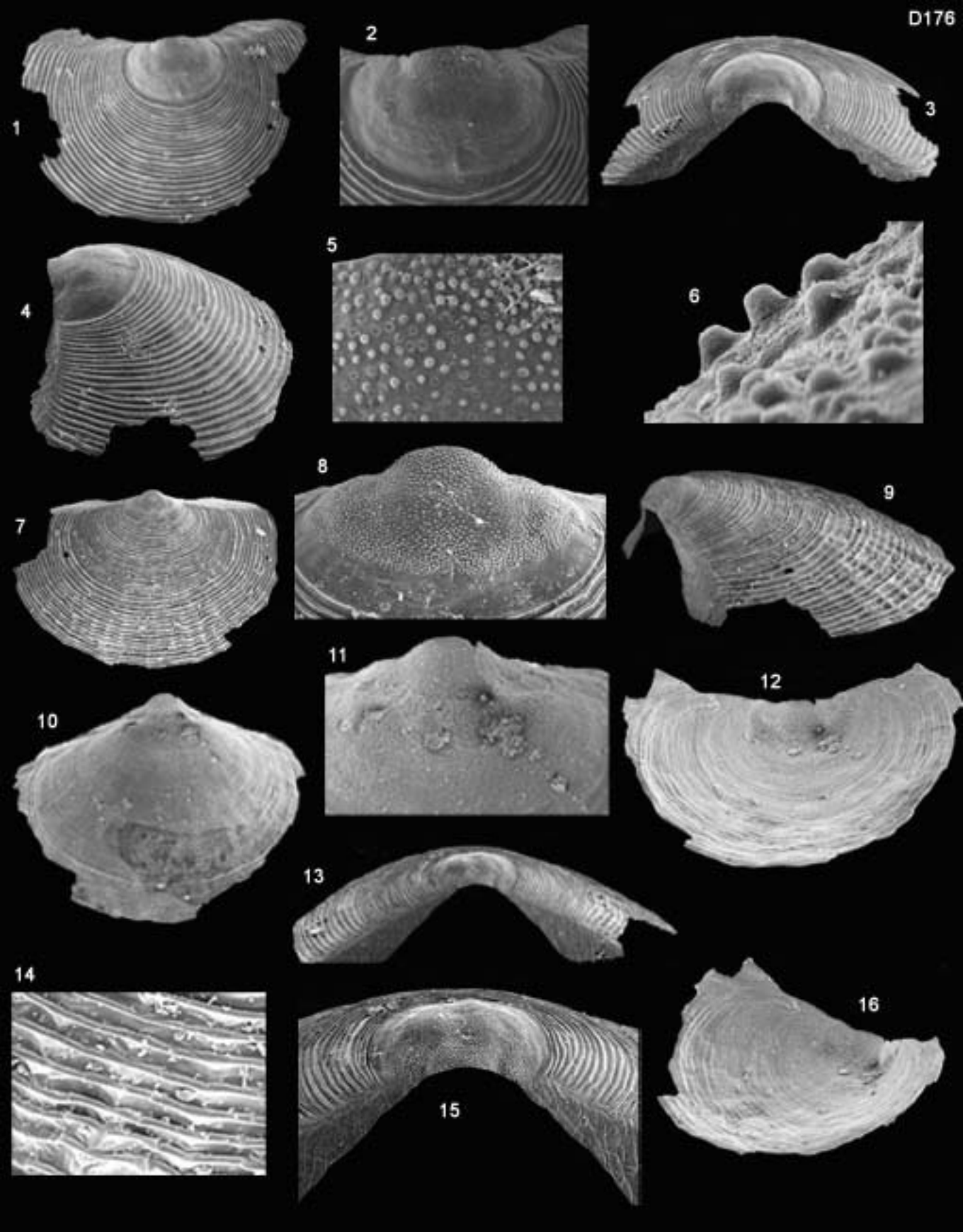
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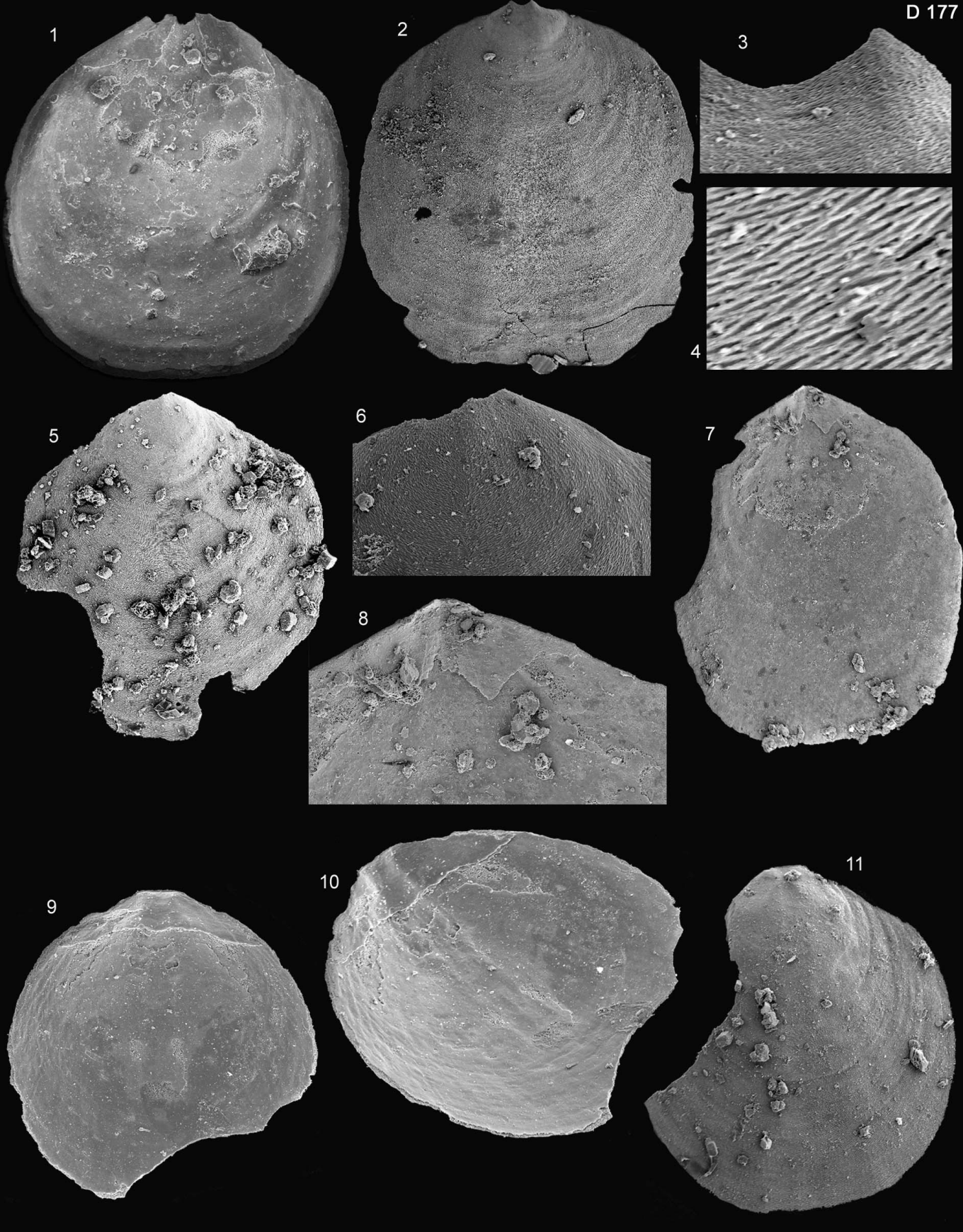
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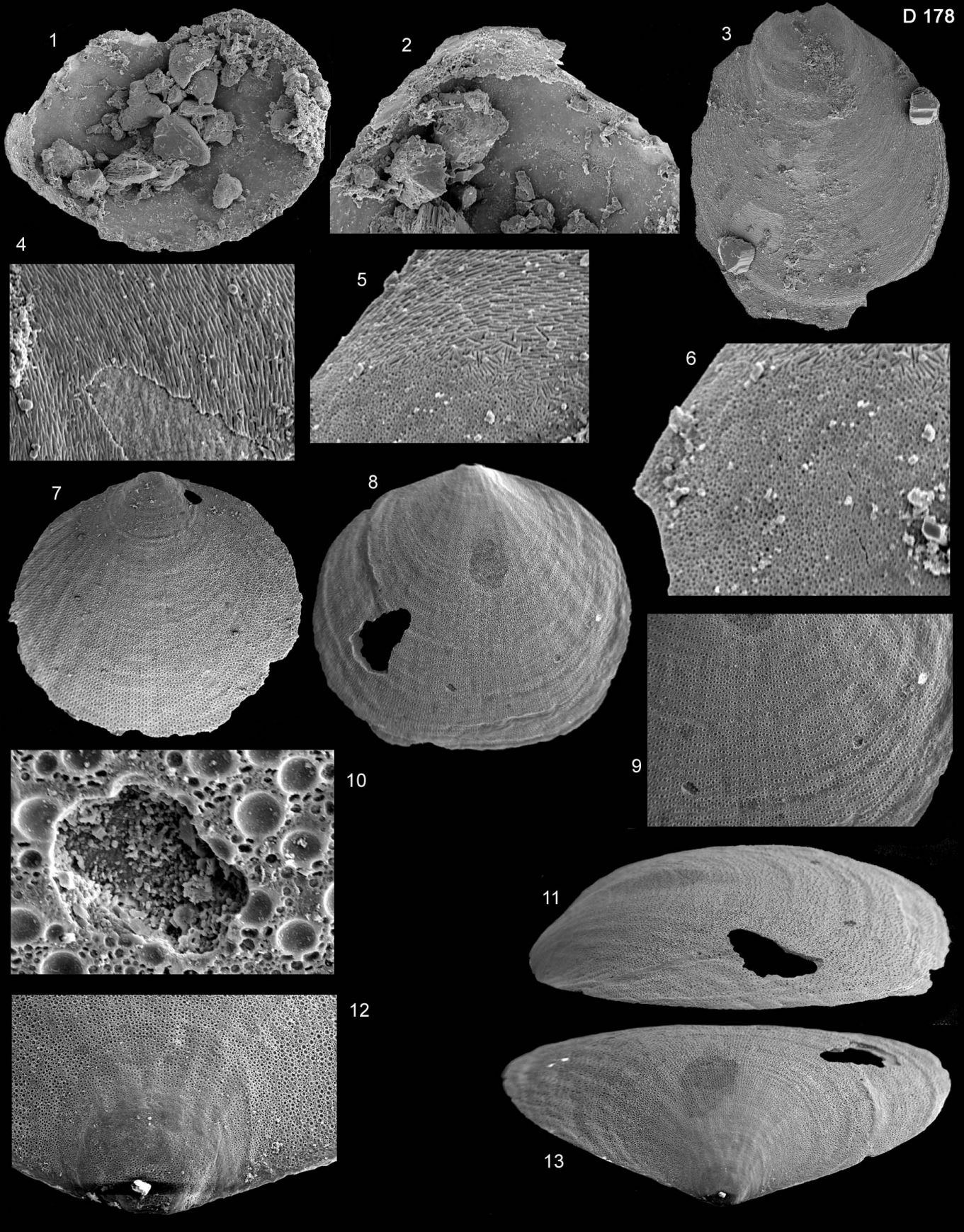
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Conclusion

This thesis provides an important contribution to our understanding of the linguliformean faunas in the Williston Basin. Linguliformean brachiopods are important constituents of lower Palaeozoic benthic communities, particularly in the Cambrian and Ordovician, and are found worldwide in a wide variety of facies. Despite their potential importance for biostratigraphy, palaeoecology, and palaeobiogeography, they remain largely neglected and are studied by only a small number of palaeontologists. Linguliformean biostratigraphy remains limited and, because they are so poorly known from many areas in the world, their value in correlation is uncertain. Likewise, their value in palaeogeographic reconstruction remains untested, but because of their long planktotrophic larval stage, and the cosmopolitan distribution of many species, they have great potential in this regard. It is not known how linguliformeans respond to environmental change, but they appear not to have been greatly affected by the Late Cambrian extinction events that devastated the trilobites. Improved understanding of linguliformean palaeoecology may improve our understanding of extinction events.

Linguliformean brachiopods were previously unknown from the Deadwood Formation in Western Canada and poorly known in the United States. Though the epeiric sea in which the Deadwood Formation was deposited was a major zoogeographic region of Laurentia during the Cambrian it has remained poorly understood. The Deadwood Formation in Canada is poorly fossiliferous, and this study provides the first reliable age for any part of the formation in Canada. From the subsurface of Alberta and Saskatchewan, twelve species are described, of which two are new, and are assigned to eight genera. The new subfamily, Neotretinae, is erected to emphasize the evolutionary

relationship between the genera *Neotreta* and *Rhondellina*, which are more closely related to each other than any other acrotretid genus. Additionally, *Linnarssonella elongata* Bell, 1941 is reinstated as a valid species, arguing that the morphological species concept does not depend on geographical or temporal distinctiveness, and that non-sexual morphotypes of a single species are unlikely to retain fidelity within the same geographical region. Because they represent the only fossils recovered from the Deadwood Formation in Canada, aside from occasional, non-diagnostic conodonts, they have potential relevance to petroleum exploration. From the Black Hills of South Dakota thirty-six species are described, of which fifteen are new, assigned to twenty-three genera, of which five are new. Three of the new genera belong to the family Zhanatellidae, increasing the number of genera in this family by more than twenty-five percent. In addition to species of these three new genera, a new species of the zhanatellid genus *Tropidoglossa* was described, and two undescribed zhanatellid species belonging to unknown genera were found. Zhanatellids are distinguished by the presence of pits in both the larval and postlarval shells, and the unusual abundance and diversity of zhanatellid species in the Deadwood Formation of South Dakota is likely to have ecologically significant, which, at present, remains uncertain. A new lingulid family, Holmerellidae is also erected, containing three new species that are unique among the Linguloidea in possessing a pitted larval shell and a smooth postlarval shell. This study expands the geographical range of existing species, further demonstrating the cosmopolitan distribution of some linguliformean taxa, and improving the capacity for international correlation of early Late Cambrian strata.

The recovery of a large number of valves with predatory perforations demonstrates that not only boring predators attack linguliformean shells, and allowed the development of a model for various attack modes that could have been used to create different types of perforations. This model could, presumably, be applied to predatory perforations in any shelled fossil. As more fossils showing signs of predation are collected, the model can be refined, increasing its utility. This is important because Cambrian ecosystems are difficult to reconstruct and predator-prey relationships and their relationship to the Cambrian radiation are virtually unknown. The recovery of so many preyed upon valves was unexpected and suggests far more dynamic interactions in Cambrian ecosystems than has been previously known.

Based on previous taxonomic descriptions, linguliformean brachiopods from the Deadwood Formation were thought to represent endemic faunas, similar to most polymeroid trilobites in the Cambrian. Endemism in this region is also a logical conclusion given the vast inland sea in which the Deadwood Formation was deposited, yet half of the genera present have cosmopolitan distribution. The occurrence of several taxa characteristic of Australia and Kazakhstan suggests possible migration routes for the planktotrophic linguliformean larvae. A hypothetical map demonstrating the possible orientation of large scale ocean circulation patterns in the Late Cambrian is proposed and can be refined as more information on the distribution of linguliformean taxa becomes available. The long plankotrophic stage of linguliformean larvae gives the group the potential to be useful tools for reconstructing palaeo ocean currents. Further research along these lines could focus on linguliformean larval distribution, such as determining whether there is a link between the morphology of a species' larval shell pits and the

range of its distribution, and increased understanding of linguliformean palaeobiogeography may help to refine plate tectonic and palaeo-oceanic reconstructions.

Many lingulid species have small or no pits in their larval shells. It may be no coincidence that many lingulids tend to be endemic and have only limited geographical range. Acrotretids, on the other hand seem to be more consistently cosmopolitan in their distribution, and this group is characterized by the pitting of its larval shells. It is interesting to note that lingulids of the family Zhanatellidae are extensively pitted in both the larval shells. If pitted shells do, indeed, represent an adaptation to increase buoyancy then it may be that zhanatellids were epibionts, living attached to other, possibly planktic, organisms. The fact that zhanatellids have pedicles argues against a free-swimming lifestyle, but improved buoyancy could have better enabled them to hitch rides on other organisms, thereby increasing the range of their distribution. It should be noted, however, that several of the zhanatellids described in this study possessed small, obliquely angled punctae rather than the more typical hemispherical pit, and do not appear to have any relation to buoyancy.

Another potential avenue for further research would be to plot the occurrence of each linguliformean species to see whether any distribution patterns can be determined. If so, then refined palaeocurrent maps can be constructed with far greater detail than the one included in this thesis.